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OBSERVATIONS ON NOCTURNAL ACTIVITY IN SOME AFRICAN TABANIDAE (DIPTERA)

By A. J. Haddow and Philip S. Corbet
(*The East African Virus Research Institute, Entebbe, Uganda*)

Members of the East African Virus Research Institute are at present engaged in a detailed study of the behaviour of biting Diptera in a small forest in central Uganda. The work is being carried out at various levels on a steel tower which rises through the canopy to a height of 120 feet, the studies being based on baited catches and on trapping at mercury-vapour light. As a preliminary to the light-trap work, various series of trials were carried out in the Institute grounds at Entebbe to find what type of light-trap was most suitable and which anaesthetic was fastest and most potent. The standard Robinson-type trap with 125-watt bulb (Robinson and Robinson, 1950) was taken as basic, and various modifications were tested. It is not proposed to discuss these here. It may be mentioned in passing that among anaesthetics and poisons tried the only substances which proved really effective were tetrachlorethylene ($CCl_2 = CCl_2$), trichlorethylene ($CCl_2 = CHCl$) and tetrachlorethane ($CHCl_2$—$CHCl_2$). Tetrachlorethylene, apart from being the fastest in action of the three, is also much cheaper than the others, at least in East Africa.

During the particular series of 23 catches which will be discussed in detail below, the trap in use was a Robinson trap with the addition of a horizontal metal roof, slightly greater in diameter than the trap itself. This prevented light from passing directly upward, while permitting a broad belt of light to be cast out sideways in all directions. In addition, the trap was shielded by three-eighths inch wire mesh screening to exclude the larger insects. The primary object of the work being to study entry to the trap, it was necessary that even the most resistant species should be knocked down at once. Accordingly, on the 23 trap-nights discussed anaesthetic was not employed—insects entering the trap simply dropped into a deep beaker of alcohol which fitted snugly below the entry-cone, as in the work of Corbet and Tjønneland (1955). During most of the other work which is commented on anaesthetic was used instead of spirit.

The compound in which the work was carried out consists of 30 acres of hilltop, the highest point being about 300 feet above the level of Lake Victoria. To the north and north-west of the hill is a major arm of the lake, the distance to the water's edge being about three-quarters to one mile. To the north-west lies an extensive reed and papyrus swamp, at a distance of a little over half a mile. Along the border of this swamp is a narrow belt of swamp-forest. To the south lies a similar swamp, at a distance of half to three-quarters of a mile, but here there is no fringing forest. To the east and south-east is a hilly area, rather bare of trees, and the main part of Entebbe township. All round the Institute compound are African plantations and vegetable gardens—bananas, cassava and coffee being favoured crops. The compound itself is mainly close-cut lawn with houses in their large gardens, laboratories and animal colonies, and groups of well-grown trees.

During the trials the traps were run from one hour before sunset till one hour after sunrise and, though various sites were used, the yield of tabanids was at first too small to excite much attention. The main point of interest was that specimens of *Chrysops centurionis* Austen were obtained, including males. The female of this species bites almost exclusively in the forest canopy in the hour after sunset (Haddow *et al.*, 1950; Haddow, 1952; Duke, 1958). These first catches showed, however, that both sexes may range at least half a mile beyond the forest edge and that they may rise to considerable height (the nearest known habitat and probable breeding-place of this species being the belt of swamp forest north-west of the Institute and about 250–300 feet below the compound).

Finally, a very favourable spot was found in one of the gardens, in a sheltered corner of the compound. This garden is surrounded by a dense cypress hedge about five feet six inches high, and there are numerous large trees in and around it. It has been stated by Thorsteinson (1958) that " Tabanid flies display an exceptionally strong tendency to orientate to and congregate in enclosures which accumulate heat during daylight ". The present work bears out this contention and, briefly, it may be mentioned that our work suggests that the position of the trap is much more important than its exact pattern or the type of mercury-vapour lamp used. We have not noted significant differences between catches made with " black light " and ordinary frosted mercury-vapour bulbs. On the other hand, a change in position of only a few yards may have a most marked influence on the yield.

A trap was placed in this favourable spot, at a height of approximately 2 feet 6 inches above ground level, and at once significant numbers of tabanids began to be taken nightly, males predominating. This Institute has for many years been interested in nocturnal activity in this group. After the discovery, mentioned above, that *C. centurionis* bites after dark, it was found that various other species might sometimes be taken by night, and it was pointed out by one of us (Haddow, 1952) that of 29 Uganda species studied, 12 had exhibited crepuscular or nocturnal activity. As two of these 12 were later considered to be synonymous, the amended number was 11. These were: *Haematopota nefanda* Edw., *H. guineensis* Bigot, *H. patellicorne* Enderlein, *Tabanus xanthomelas* Austen, *T. par* Walker, *T. thoracinus* Pal. de Beauv., *T. conformis* Walker, *T. taeniola* Pal. de Beauv., *Chrysops centurionis* Austen, *C. funebris* Austen and *Tabanocella perpulcra* Austen. In the same paper a personal communication from Dr. J. Bequaert was quoted, to the effect that various American species (including *Bolbodinyia bicolor* Bigot, *Chlorotabanus inanis* Fabr., *C. mexicanus* L. and *Dichelacera vespertina* Bequaert and Renjifo-Salcedo) were also crepuscular or nocturnal. Further to this, we recently received from Dr. C. B. Williams a note describing several large night catches of *C. inanis*, made by him with acetylene light in British Guiana in 1916. It has already been suggested that the remarkable eyes of tabanids, and particularly of the males, might have some relation to nocturnal activity and perhaps to mating (Haddow *et al.*, 1950).

Interest was immediately aroused by the fact that a large part of the catch was made up of members of a well-known " species pair ", *Tabanus par* Walker and *T. thoracinus* Palisot de Beauvois. Both are common round Entebbe and, though they do not often bite man in this area, frequently enter houses, motor-cars, etc. Females of *T. par* have been taken biting in the forest canopy by night and in the forest at ground-level by day, and females of *T. thoracinus* have been taken biting in the forest at ground-level by day, while males have been taken at lamps in the canopy by night, as noted in the papers referred to above. Obviously, however, man is not a preferred host of either species in this area, and it is interesting to note that Crosskey and Crosskey (1955) record *T. par* as a species attracted to cows and camels in West Africa.

As soon as satisfactory numbers began to appear in the traps it was decided that hour-to-hour collections should be made to investigate activity patterns. This was done on 20 successive nights. On the last three nights two traps were run, one with the ordinary frosted glass bulb and the other with a " black light " bulb of the same wattage. There are thus 23 trap-nights for which detailed information is available, the run extending from one hour before the actual time of sunset (which, following Lumsden (1952), is always given as 18.00 hours) till one hour after sunrise. On one day of the series the trap was run continuously for 24 hours to find whether tabanids could be attracted by day, but only a few tiny non-biting Diptera were obtained. Throughout the series no tabanids were taken before sunset or after sunrise, whereas the number taken by night was 523, specimens being obtained on every night of the series. On one night the trap was run without the horizontal metal cover, to find whether increased numbers of tabanids would be taken. This did not occur, the number being much the same as on the preceding and succeeding nights. The results are shown in Table I and figure 1, and may now be discussed.

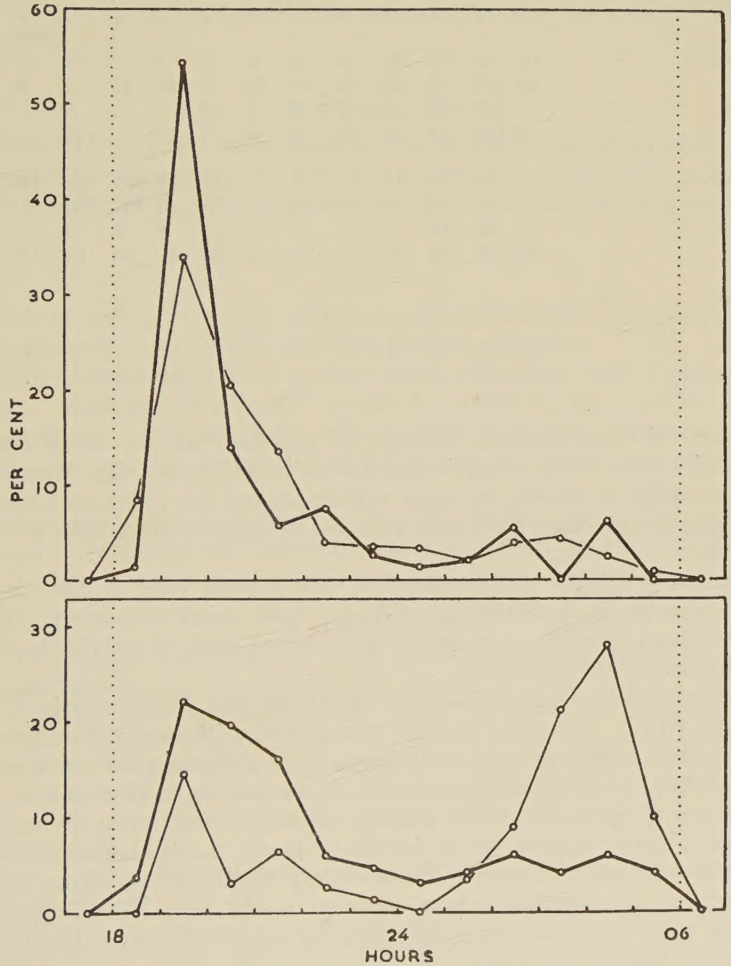

Fig. 1.—Nocturnal flight patterns of *Tabanus par* (above) and *T. thoracinus* (below). The figures are geometric means expressed as percentages to facilitate comparison. (*Thin line,* males; *thick line,* females.)

In the case of *T. par* and *T. thoracinus* geometric means have been worked out, following the practice of C. B. Williams (1937).

Among the scarcer species the occurrence of males of *Ancala fasciata nilotica* Austen may be noted as rather remarkable. The larvae of this species are associated with the water cabbage (*Pistia stratiotes* L.), and there are no beds of this plant within a mile of the Institute. The females are, in Uganda, closely associated with the Lake shore and this also applies in other countries (see the summary on this subject by Oldroyd, 1954). The present evidence, however, suggests that males at least may wander much further from water than had been expected.

TABLE I.—*Catches of Tabanids at mercury-vapour light,* 23 *trap-nights, Nakiwogo, Entebbe, Uganda*

(*M*, male; *F*, female; Geometric means (M_G) have been multiplied by 100 to give integer numbers)

	Hour														Totals
	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	06–07	
A. fasciata nilotica															
M, Totals	.	.	.	2	.	1	.	.	.	.	.	.	.	.	3
T. par															
M, Totals	.	13	44	26	20	5	4	4	3	5	5	3	1	.	133
$100 M_G$	.	34	132	80	53	15	13	13	8	15	16	9	3	.	.
F, Totals	.	1	47	12	6	7	2	1	2	4	.	5	.	.	87
$100 M_G$	.	3	132	34	14	18	6	3	5	13	.	15	.	.	.
T. thoracinus															
M, Totals	.	.	26	6	11	5	2	.	7	19	37	48	19	.	180
$100 M_G$	.	.	77	16	34	13	6	.	18	47	111	146	51	.	.
F, Totals	.	4	28	19	16	7	5	3	4	6	4	6	4	.	106
$100 M_G$	.	11	68	60	50	18	15	9	13	18	13	18	13	.	.
T. fraternus															
M, Totals	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
C. centurionis															
M, Totals	.	1	4	1	1	.	1	1	.	.	.	2	1	.	12
F, Totals	.	1	3	1	.	.	.	.	.	.	.	.	.	.	4

In the case of *C. centurionis*, though the numbers are too small for detailed discussion, there seems to be a preference for the second hour after sunset. This is of interest, as biting is known to occur mainly during the previous hour. It was interesting also to note that there was evidence of male activity later at night and again at dawn.

T. par was exceedingly well represented with a total yield of 220, the ratio of males to females being approximately 1·5 : 1. Both sexes were active throughout the night, and both showed an extremely well-marked peak of activity in the second hour after sunset (19–20 hours).

In the closely-allied *T. thoracinus* the total yield was 286, the ratio of males to females being 1·7 : 1. Here the pattern was entirely different. The females once again showed their highest activity in the hour 19–20, but the peak was really spread over the three-hour period 19–22 hours. The most striking difference was, however, in the behaviour of the males, which showed only slight activity in the early part of the night, and a major peak in the period 03–05 hours, shortly before sunrise, which occurs at approximately 06 hours. These closely allied species, whose distribution overlaps very considerably and whose recorded habits have till now seemed very similar, have thus shown a major difference in behaviour where the response to mercury-vapour light is concerned.

It may be of interest to list the total yield of tabanids taken at mercury-vapour light at all stations and with all types of trap within the Institute compound. There have been 82 trap-nights to date, and the yield has been approximately 10 tabanids per trap-night, the species being as follows:

Species	Males	Females
A. fasciata nilotica Austen	3	.
T. par Walker	219	125
T. thoracinus Pal. de Beauv.	297	163
T. fraternus Macquart	1	.
C. centurionis Austen	22	7
Totals	542	295

In conclusion it may be mentioned that work on the high forest tower is now in progress. *C. centurionis* has been taken biting, and also in traps, up to the highest level above the canopy (120 feet). *T. thoracinus* males and females have also been trapped at 120 feet. In addition, other species of *Tabanus, Tabanocella* and *Thaumastocera* are being taken at the highest levels—all by night. An even more interesting observation has been that tabanids of at least three species swarm very actively over the tower just before sunrise, in the period 05–06 hours. They are usually too high above the observer for capture and even when low are extremely difficult to net. Only three have been taken so far and these all proved to be male *T. thoracinus*.

ACKNOWLEDGMENTS

We wish to thank Mr. John Bowden, Senior Entomologist (Agriculture) Uganda Protectorate, for suggesting the use of tetrachlorethane and for making available a supply, and Mr. G. A. H. McClelland for help in some of the later catches.

SUMMARY

The use of mercury-vapour light in modified Robinson traps has revealed considerable nocturnal activity in some East African tabanids.

The two commonest species in the catches concerned were *Tabanus par* and *T. thoracinus*. Males and females of *T. par* showed a major peak of activity in the second hour after sunset. Females of the closely allied *T. thoracinus* showed rather similar behaviour, but here the main peak of activity in the males occurred shortly before sunrise.

Evidence of nocturnal activity above the forest canopy by various tabanid genera, and of swarming just before sunrise in this zone are discussed briefly.

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OBSERVATIONS ON THE FEEDING AND MATING OF *CULICOIDES CIRCUMSCRIPTUS* KIEFFER (DIPTERA : CERATOPOGONIDAE)

By P. Becker

(*Royal Horticultural Society's Gardens, Wisley, Ripley, Surrey*)[1]

FEEDING

Unlike most of the other members of the genus, *Culicoides circumscriptus* Kieff. has not been recorded as a blood-sucking species. During the course of several years' study of the species many samples of midges were caught in its salt marsh habitats while biting the author or flying around grazing cattle. None of the species caught proved to be *C. circumscriptus*. Further, no female of this species captured in the field has ever shown traces of having had a blood meal. Dissection has invariably revealed that the gut contained, if anything, only a clear fluid, colourless or slightly amber.

Attempts to induce biting have also failed. Glass tubes containing female midges, both wild and laboratory-reared, were inverted on the skin of the forearm. Females were also kept in an open pill-box strapped to the arm for periods of up to 24 hours. The author's arm was also inserted through the muslin sleeve of a cage containing midges and kept there for long periods at all times of the day and night. On no occasion was there any attempt to bite. Birds were also tested as possible hosts, the midges being given the opportunity to feed on pigeons and young chicks, and, on the chance that they might have the same entomophagous habit as some other Ceratopogonidae (*see* Edwards, 1923), they were also enclosed in a cage containing a selection of insects obtained by sweeping with a net in the salt marsh habitat, but feeding did not take place.

The clear fluid, which was found in the mid-gut and oesophageal diverticulum of many wild female midges, was analysed by the paper chromatography technique for sugars described by Block *et al.* (1955) ; 12 excised guts were placed on the paper in line with 12 excised guts of unfed laboratory-reared insects (control) and sucrose, fructose and glucose were used as standards. Each of these sugars, the constituents of nectar, were found to be present in the guts of the wild midges.

These observations and experiments indicate strongly that the females of *C. circumscriptus* do not suck blood, and this suggests the possibility that the species is autogenous, laying eggs without a blood meal. The number of eggs laid in the laboratory by 55 wild-caught females varied from 45 to 401 (average, 252). This is considerably greater than the numbers reported for other species which are known to take a blood-meal (Table I). However, Downes, in a private communication, states that among the autogenous Canadian species reported by him (Downes, 1958*b*) a single female of *C. gigas* Root and Hoffman laid 242 eggs, and a female of a new species laid 300 eggs. He has also found that in Britain *C. riethi* Kieff. is autogenous, and a batch of 244 eggs was laid by one female. It cannot be supposed, therefore, that among *Culicoides* autogenous batches of eggs are smaller than those laid after a blood meal, as has been reported for some species of mosquitoes (Bates, 1949 ; Hocking, 1952).

Among the autogenous species the source of the considerable amounts of nutriment required to produce such large numbers of eggs is not known with any certainty. Among mosquitoes it has been suggested (Marshall, 1938) that the larvae store up exceptional quantities of fat-body which are carried forward to the adult stages. Downes (1958*b*) implies that this may also be the case among *Culicoides,* but comparison of the larvae of *C. circumscriptus* with those of blood-sucking species does not indicate that the fat-body is exceptionally developed. Hocking (1952) showed that an autogenous race of *Aëdes communis* De Geer obtained the necessary nutriment by autolysis of the flight muscles. Gravid females of *C. circumscriptus* have, however, been caught in flight and sections of the thorax of parous females have shown the flight muscles still intact.

---

[1] This work was carried out at the Zoology Department, University of Glasgow.

TABLE I.—*Comparison of the number of eggs laid by various species of* Culicoides

Species	Reference	Number of eggs
C. nubeculosus . . .	Roberts (1950)	Av. 380*
,, ,, . . .	Lawson (1951)	More than 200
,, ,, . . .	Megahed (1956)	Av. 135
C. pulicaris	Parker (1949)	Av. 93
C. impunctatus . . .	Hill (1947)	30–65
C. obsoletus	,, ,,	Av. 75
C. odibilis	,, ,,	Av. 80
C. oxystoma . . .	Patel (1921)	Up to 156
C. tristriatulus . . .	Williams (1951)	42–81
C. austeni	Sharp (1923)	90–141
C. circumscriptus . . .	Becker (present paper)	Av. 252

* Megahed (1956) suggests that this number may represent more than one batch of eggs.

Since it has not been possible to obtain eggs from laboratory reared females of *C. circumscriptus,* no conclusive evidence of autogenous egg production can at present be obtained for this species. There can be no doubt that such behaviour would be distinctly advantageous in the salt marsh habitat where, as is pointed out elsewhere in this paper, conditions are such that flight is impossible for a large part of the time, so that the opportunities of obtaining a blood meal are limited.

There still remains the possibility, in spite of the negative results of the laboratory experiments, that, as is the case in many other genera of the Ceratopogonidae, *C. circumscriptus* attacks other insects, and that some, at least, of the clear fluid found in the alimentary canals is insect blood. It is also remotely possible that the necessary nutriment is obtained from a plant source. Downes (1955*b*) has shown that this is the case in *Atrichopogon pollinivorus* Downes, the female of which pierces the pollen grains of honeysuckle and sucks out the sap. Both these suggestions, however, are entirely speculative and are not supported by any evidence whatsoever.

The results of chromatographic analysis of the contents of the alimentary canal strongly suggest that nectar is ingested by both sexes as a source of energy. This habit has been reported in many blood-sucking Nematocera. Among *Culicoides* spp. it has been demonstrated by Downes (1955*b*, 1958*b*), Kieffer (1923) and Knoll (1922). The flowering plants in the vicinity of the breeding area at Dumbuck, near Dumbarton, have all been examined carefully on many occasions but only seldom have midges been seen on them. At no time has feeding been observed. The numbers of midges caught by sweeping these flowers with a net did not differ markedly from the numbers taken on other vegetation in the vicinity. Apart from the imperfections of the observer, the explanation for this lack of observations of nectar-feeding, despite the positive evidence in the alimentary canals, may be that it possibly takes place largely after sunset, when the midges have ceased to fly and have settled on the vegetation.

Another likely source of carbohydrates is honey-dew deposited by aphids on the vegetation. Large numbers of aphids are found on the reeds on the marsh, and in hot dry weather the leaves become thickly coated with honey-dew. No observations have been made which might support this suggestion, but it is unlikely that such an easily-won sugar meal would be ignored by the midges. Nielsen and Greve (1950) are of the opinion that some Culicids feed on honey-dew. Gad (1951) observed females of *Culicoides obsoletus* (Meig.) " on leaves and trunks of trees lapping drops of sap ".

MATING

Those working with the genus *Culicoides*, other than *C. nubeculosus* (Meig.), have always had great difficulty in maintaining laboratory cultures beyond one generation. The main obstacle has been the refusal by the adults to mate in captivity. Similar difficulties were experienced with *C. circumscriptus*. Mating did not take place when laboratory-reared adults were kept in " Perspex " cages or glass tanks and supplied with water and moistened chopped raisins, or when Megahed's (1956) method of obtaining mating of *C. nubeculosus* in 3-inch by 1-inch tubes was tried.

In an effort to persuade the midges to fly about the cage and mate, air was passed gently through and the cage also placed above a continuous moving band of black and white striped cloth, but without success. The feeding experiments mentioned earlier were also watched for evidence of mating, since it has been observed that with some mosquitoes (Howard *et al.*, 1913 ; Bates, 1949), with *C. nubeculosus* (Pomerantsev, 1932) and with *C. utahensis* (pars) Fox (Downes, 1958*a*) the host animal exerts some attraction for the male as well as the female, and acts as a rendezvous for mating purposes. On no occasion, however, was mating observed, and no spermatozoa were found in the spermathecae of dissected females.

In the field a close watch has always been maintained for indications of breeding behaviour, but none have been seen. Downes (1955*a*) has demonstrated swarming behaviour in eight species of *Culicoides* and has shown that in *C. nubeculosus*, *C. riethi* and, probably, *C. impunctatus* Goetgh. and *C. obsoletus* mating occurs within the swarm. Many such swarms have been observed on a number of salt marshes and they have been induced to form by means of artificial markers, but on no occasion have they been found to consist of *C. circumscriptus*. Neither does Downes record any instance of swarming in this species, although many of his observations were carried out in areas where it is abundant. It is fair to assume, therefore, that *C. circumscriptus* does not swarm, and that mating probably occurs while the flies are at rest among the vegetation. Although swarming is a widespread habit among the Nematocera, copulation has been observed to occur while at rest in *Anopheles maculipennis* Meig. var. *atroparvus* (Cambournac and Hill, 1940), *Atrichopogon pollinivorus* (Downes, 1955*a*) and in *Culicoides nubeculosus* and *C. riethi* (Pomerantsev, 1932 ; Downes, 1955*a*). Downes (1958*a* and *b*) also describes three Canadian species of *Culicoides* which mate on the ground or on vegetation and have not been observed to swarm. Modifications of the male antennae of two of the species as well as of *Atrichopogon pollinivorus* strongly suggest that the power to mate in flight has been lost.

Most salt marshes are extremely exposed to winds from all quarters and, as has been observed by many workers, *Culicoides* will fly only in calm conditions or in sheltered locations. Downes (1955*a*) has stated that the flight of *C. nubeculosus* and *C. riethi* ceases when the wind is above an estimated speed of 2–3 m.p.h. For *C. circumscriptus* the figure is probably much less, as it has been found difficult to catch them in flight even in the lightest of breezes. The ability to mate at rest, therefore, is of distinct advantage to a species in whose habitat periods of calm are severely limited. In this connection, it is of interest to note that the average proportion of males caught by aerial netting was only 7 per cent., whereas the number of males caught by sweeping vegetation amounted to an average of 27 per cent. of the total.

The fact that other salt marsh species do form swarms does not invalidate this hypothesis. Considering the different types of mating behaviour found in *C.*

nubeculosus and *C. riethi*, it is not improbable that these other species may also mate without swarming, particularly when conditions are unfavourable for flight.

Cambournac and Hill (1940) are of the opinion that the sexual significance of swarming in *Anopheles maculipennis* var. *atroparvus* is only vestigial. There is some evidence also that in other species scattered throughout the Nematocera the habit has been lost or is in the process of dying out. Among those whose breeding habits are well known, various species exhibit patterns of sexual behaviour which would appear to represent various stages in this process of evolution away from the typical swarm-mating behaviour. Thus, while in the majority of mosquitoes mating takes place in the swarm :

(1) in *Aëdes aegypti* L. the males may seek out the females individually, though swarming is more common (Howard, Dyar and Knab, 1913);

(2) *Aëdes cantans* (Meig.) forms swarms but mating seldom takes place in them; mating takes place in solitary flight or among vegetation (Nielsen and Greve, 1950);

(3) with *Culicoides riethi* mating takes place in swarms, but on rare occasions it has been seen to copulate while resting (Downes, 1955*a*);

(4) *Culicoides nubeculosus* is able to mate equally easily either in swarms or at rest (Pomerantsev, 1932 ; Downes 1955*a*);

(5) *Anopheles maculipennis* var. *atroparvus* mates, as a rule, while at rest; swarming occurs, but only occasionally does mating take place in the swarm (Cambournac and Hill, 1940);

(6) *Atrichopogon pollinivorus*, *Culicoides utahensis* (pars), a species of the *C. nubeculosus* group, and a species close to *C. alaskensis* Wirth mate at rest; they appear to have lost the habit of mating in flight and the male antennae of all but the last species are modified in such a way as to suggest that this would be difficult or impossible (Downes, 1955*a* and *b*, 1958*a* and *b*.).

The mating habits of only two British species of Culicoides have been observed in detail (by Downes, 1955*a*). It seems likely, and is partly shown by Downes (1958*a* and *b*), that the patterns of sexual behaviour among the genus may be more complex than has hitherto been realised and that these patterns may show specific variations. For example, Downes (1955*a*) has established that *C. impunctatus* and *C. obsoletus* mate in flight, but has not observed swarming in these common species. He states that the copulating pairs seen were probably from unobserved swarms but it is equally possible that they may mate in solitary flight, as does *Aëdes cantans*. It has been shown, too, by Parker (1949), that in *C. pallidicornis* Kieff. the females do not appear until the peak of flight activity of the males is passed, and that the peaks of flight activity of the two sexes are separated by about two hours. Although the males formed swarms it is doubtful if, under these circumstances, much mating would occur. Thus it is probable that in this species, as in *Anopheles maculipennis* var. *atroparvus*, the swarming habit is vestigial and that most mating takes place at rest on the vegetation.

It is suggested that *C. circumscriptus* may belong to the category represented by *Atrichopogon pollinivorus* and the three Canadian species of *Culicoides* which have similar habits, *i.e.* that it mates while at rest in the vegetation, having completely lost the swarming habit. The antennae of the males, however, show no signs of modification, and if it mates at rest it is difficult to understand why this species refuses to mate in cages.

SUMMARY

The females of *Culicoides circumscriptus* Kieff. are not known to suck blood. Numerous attempts to induce them to do so have failed. The possibility that they are autogenous is discussed but there is no evidence to suggest the source of the nutriment required for egg-formation. It is not obtained from autolysis of the flight muscles and the larvae do not have an exceptionally developed fat-body. Chromato-

graphic analysis of the gut contents indicates that nectar is taken as a source of energy.

Experiments to obtain mating in the laboratory were unsuccessful and it has not been observed in the field. No mating swarms are formed. It is suggested that in a number of groups of the Nematocera the sexual significance of swarming is progressively diminishing and that in some species, among them *C. circumscriptus*, the habit of swarming has been completely lost.

ACKNOWLEDGMENTS

I am indebted to Professor C. M. Yonge, C.B.E., F.R.S., for the use of the facilities of the Zoology Department of the University of Glasgow. I also wish to thank Mr. J. A. Downes and Dr. J. W. H. Lawson for their helpful criticism and advice.

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THE EGG AND EARLY STAGES OF *LESTINOGOMPHUS AFRICANUS* (FRASER) (ODONATA : GOMPHIDAE)

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and

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In June, 1955 one of us (R. M. G.) obtained two female specimens of *Lestinogomphus africanus* (Fraser) taken flying beside a small running stream near the village of Kuru, N. Nigeria (situated on a plateau 4000 feet above sea level). They shortly afterwards deposited batches of eggs in captivity. The specimens were captured by hand by village children who had joined in the hunt, so that unfortunately the behaviour during natural oviposition was not observed. The first batch of eggs was laid in the paper triangle in which one of the females was confined, shortly after capture. This egg mass was dropped into a tube full of water from the same stream, and the eggs quickly separated. Preliminary examination with a pocket lens showed what appeared to be a cap or plug at each end. The abdomen of the specimen which had laid the eggs was then dipped into the water in the same tube, and a further batch of eggs was laid.

On arrival back at the laboratory, the second female was induced to oviposit into another tube full of water from her native stream. When the eggs were examined microscopically it was found that those in the second tube had conglomerated into a single cluster, joined together by a coiled filament arising from the posterior pole of each egg. The free end of each filament had become entangled with those of the others. In the first tube, half the eggs were tangled into a similar mass, and the other half were free. The latter had the filament wound into a tight coil which was closely applied to form the cap originally noticed at the posterior end. (The apparent plug at the anterior end was a protuberant structure which will be described below.) It is presumed that these free eggs were those which had been laid on the paper, and that the filament had been fixed in the coiled position by the slight drying that had taken place before they were placed in water. In the remainder the filament had presumably uncoiled on contact with the water, and as the eggs were enclosed in a confined space they became entangled in a single cluster. There is no evidence that such clusters are formed when the eggs are laid under normal conditions, and if laid into running water it is more likely that they would be washed away singly or in small groups and the filaments become entangled in vegetation or other obstruction.

As it was not expected that time would permit the rearing of the eggs to the adult stage in Nigeria, one batch was divided and half the eggs sent to England by air to the second author (A. E. G.). However, the young larvae proved difficult to rear, and none survived beyond the third instar. In Nigeria, only second instar larvae were obtained. A brief note on these eggs was recorded at the time (Gambles, 1956), and fuller descriptions are now given of both the eggs and the young larvae.

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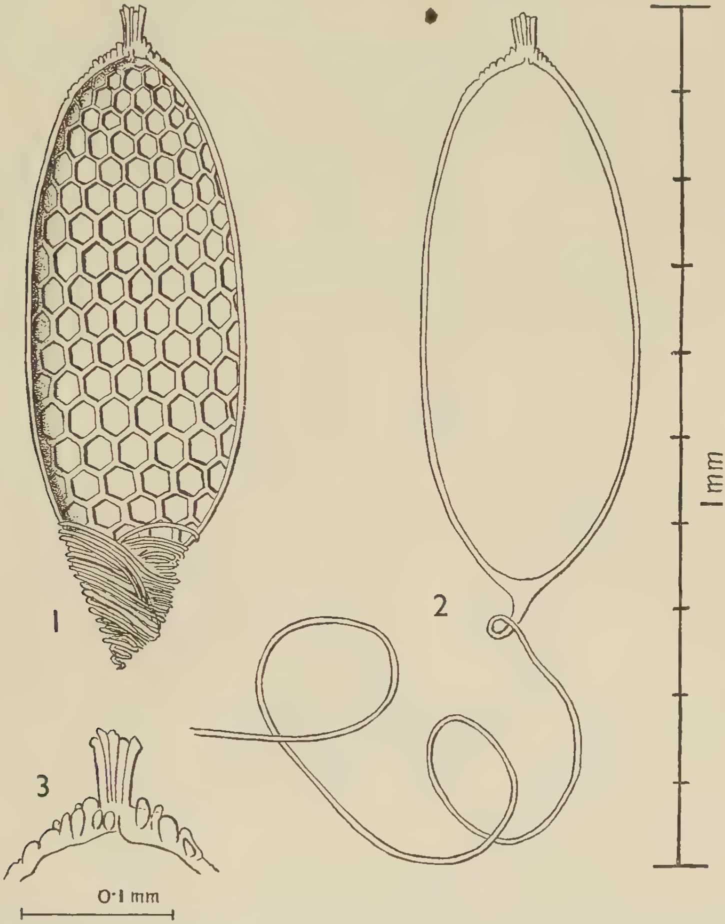
I. The Egg (*By R. M. G.*)

The egg (figs. 1–2) is ellipsoidal in shape. At both ends the chorion is tuberculated and at the anterior, or micropylar, pole there is a projecting structure that may be likened to a faggot of sticks. These sticks appear to be eight in number and the micropylar aperture probably runs between them, although this has not actually been demonstrated. The tubercles increase in size as they approach the base of the projecting bundle, and the " sticks " may represent greatly elongated tubercles, but there is no gradation between the two, those of the bundle projecting far beyond even the largest of those surrounding it. The bundle is slightly wider at the far end than at its origin (fig. 3). Except at the extremities, the whole of the chorion carries a reticulated pattern of hexagonal cells about 0·035 mm. wide. At the posterior end, the pole is produced into a long coiled filament which, when straightened out, measures approximately 30 mm. in length. The width of the filament is in most parts 0·007–0·009 mm., but it is somewhat greater close to its attachment to the egg.



Figs. 1–3.—*Lestinogomphus africanus.* (1) Egg showing posterior filament coiled ; (2) egg with filament uncoiled (reticulation omitted) ; (3) anterior pole showing micropylar bundle.

The egg, measured shortly after laying without the posterior filament and anterior projection, was 0·62–0·66 mm. long by 0·25–0·255 mm. broad. (Specimens measured in England, nearer to the date of hatching, were the same length but somewhat broader, 0·312–0·343 mm.) The anterior bundle projects 0·05–0·055 mm. beyond the rest of the egg. When the filament is coiled into a cap over the posterior end, its actual extent varies considerably from egg to egg, but in those measured the cap projected 0·08–0·09 mm. beyond the posterior extremity.

In England, the first eggs hatched 19 days after being laid, and the majority hatched on the 22nd and 23rd days in water artificially heated to 20° C. In Nigeria, where eggs were kept at room temperature under local conditions, hatching started three days later than in England (the exact temperature was not recorded). The pronymphal stage was not observed, and was probably of only a few moments' duration. Many second instar larvae were seen with the elongated tenth segment of the abdomen, still shrouded in the cast pronymphal skin, caught in the longitudinal slit in the shell through which they had emerged. In spite of vigorous struggles they appeared unable to free themselves. A few were released by prising the egg-shell open with fine needles under the microscope, but most of them must have managed to escape unaided, for only two specimens were found still entrapped and dead. It seems possible that this may be an adaptation to life in flowing water and that the emerging larvae are in this way saved from being swept away by the stream, and can only extricate themselves after they have obtained a firm hold, either on some external object or on the shell itself. The deep reticulation of the shell would provide a ready foothold, and the young larvae from eggs kept in watch-glasses and Petri dishes were seen to remain on the cluster of eggs and empty shells for some days before wandering further afield.

II. The Early Larval Stages (*By A. E. G.*)

I am indebted to Mr. R. M. Gambles for sending me half the eggs of *L. africanus* obtained from a female at Kuru, N. Nigeria, on 18th June, 1955. Unfortunately, and perhaps because the natural conditions were not exactly reproduced, no larvae survived beyond the third instar.

The eggs reached me on 22nd June and were immediately immersed in a dish of water controlled at a temperature of 20° C. and well aerated by *Elodea canadensis* Mich. Hatching commenced on 7th July and reached its peak on 10th–11th. The young larvae were liberally supplied with *Infusoria* on which they were observed to feed. There were no casualties occasioned by the trapping of the young larvae in the shell at emergence. Losses were, however, severe, only three larvae surviving until the third instar which was reached on 14th–17th July. Of these, all had died by 4th August, just before the fourth instar moult, it is thought.

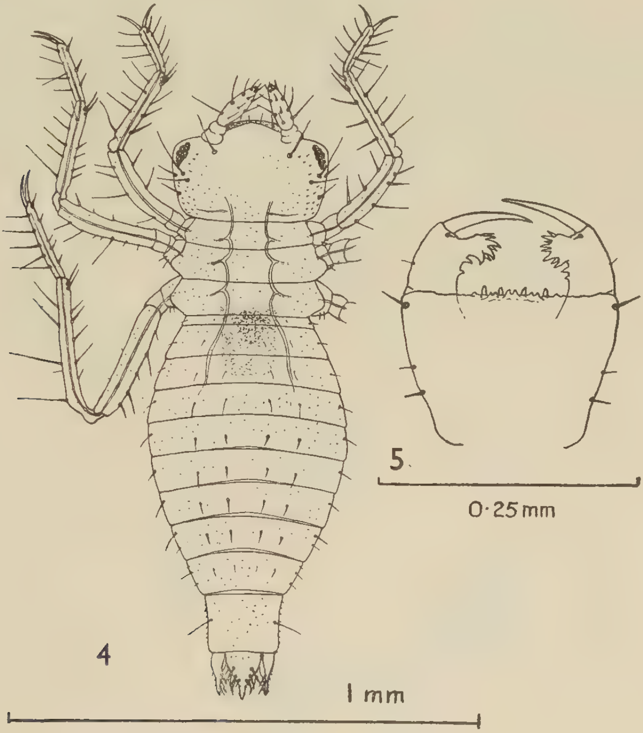
Prolarva (first instar).—Not observed.

Second instar (fig. 4).—General body-form of definite gomphine character. Length, excluding antennae but including anal appendages, 1·10 mm. Colour pale brownish, almost translucent, internal organs and main tracheae visible. Almost the entire surface covered with minute setae which appear as dark points. Head transverse in outline, front margin with marked forward protuberance, width over eyes 0·31 mm. Eyes situated at the fore corners, small and dark in colour. Head with minute setae strongest towards the lateral margins, 1 long seta located at base of each antenna, 4 on the lateral margins, that just below the eye being the longest and with a forward projection. Antennae of 3 segments, total length 0·15 mm. Scape and pedicel short and stout, flagellum about 0·11 mm. in length, stout, bearing numerous crowns of slender setae of which the basal ones are longest.

Labium (fig. 5): prementum somewhat quadrate in outline, distal margin of median lobe straight and armed with short blunt spines; lateral margins bearing 3 slender setae; labial palps with inner margins bearing 2 dentations and apically produced into a finger-like cluster of sharp dentations; movable hook curved, moderately robust; a single short palpal seta located just below the insertion of the movable hook. (It is noteworthy that the labium of *L. africanus* bears a striking resemblance to that of the second instar larva of *Gomphus graslinellus* Walsh (Needham and Westfall, 1955)).

Thorax somewhat transverse, each segment of about equal length. Legs fairly robust and of moderate length, armed with numerous setae ; tarsal combs consisting of 2 simple setae. Abdomen egg-shaped, widest at the fifth segment, tenth segment cylindrical, narrow and nearly twice the length of the ninth ; a single seta on lateral margins of segments 1–7, 2 on 8 and 9, one long and numerous short setae on 10 ; 2 mid-dorsal setae on segment 1, 4 on 2 to 9. Anal appendages of moderate length ; appendix dorsalis with apex spine-like, bearing 2 dorsal and numerous lateral setae.

Third instar.—Total length 1·33 mm. Width of head over eyes, 0·34 mm. Apart from increase in size, the only external changes appear to be confined to the labium. Inner margin of lateral palps with the 2 dentations absorbed, whilst the apical, finger-like cluster of dentations is slightly reduced in size and more blunt in outline.



Figs. 4–5.—*Lestinogomphus africanus.* (4) Second instar larva ; (5) labium.

III. Discussion,

Dr. P. S. Corbet (1955, *personal communication*) has recorded similar filaments in eggs obtained *post mortem* from the abdomen of a female *Ictinogomphus ferox* (Rambur) that had been crushed in the post, some of which he kindly forwarded for examination. These filaments are somewhat different from those of *Lestinogomphus*, and take the form of a fringe of much finer filaments surrounding a central boss at the posterior end of the egg. These are twisted to form a cord, which replaces the single filament of *Lestinogomphus*. The micropyle of *Ictinogomphus* is situated in a shallow crater which replaces the faggot-like structure. Subsequently one of us (R. M. G.) dissected a few somewhat decomposed eggs from a female *Paragomphus cognatus* (Rambur) in his collection. No trace of filaments could be found, but there appeared to be, surrounding the micropyle, a structure that corresponded to the faggot, although it was shorter than broad, more compact, and flat on the top. These structures are not figured here, as the eggs were not laid naturally. The egg of *Gomphus* itself has no filament, although it shows a small protuberance at the micropylar end (Needham and Westfall, 1955). Such filaments on the eggs of other insects with aquatic larvae are usually considered adaptations to ovipositoin in running water, and their presence in *Ictinogomphus*, which breeds in muddy ponds and lakes, may be evidence of rheophilic ancestry (Corbet, 1955, *personal communication*). *P. cognatus* has been found breeding in the stream where the present *Lestinogomphus* material was taken. In view of the occurrence of such filaments on the eggs of more than one genus in this family, their distribution in the other genera, especially when considered in relation to the breeding habitat, would be a subject worthy of further study.

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NOTES ON THE TRICHOPTERA OF A STONY STREAM

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[Communicated by T. T. Macan]

Introduction

Ford Wood Beck is a small stony moorland stream running into Blelham Tarn, which is situated on the north-west side of Windermere. The stream bed is stony almost throughout its length. The lower reach runs in a valley; station 1 is situated at the lower, and station 2 at the upper end of this stretch. At both stations the stream is nearly 2 metres wide and 10–20 cm. deep, except after heavy rain, which causes a sharp rise in level. At the upper end of the valley there is a steeper gradient, at the foot of which lies station 3. At the top of this steep stretch is a plateau and the main beck drains this area in underground channels. Station 4 is not far below the spring, which has not been known to dry up in the last 50 years. Although the slope is fairly steep, the bed has more silt than elsewhere, as there is less water particularly after heavy rain. Sykeside is a tributary that joins the main stream

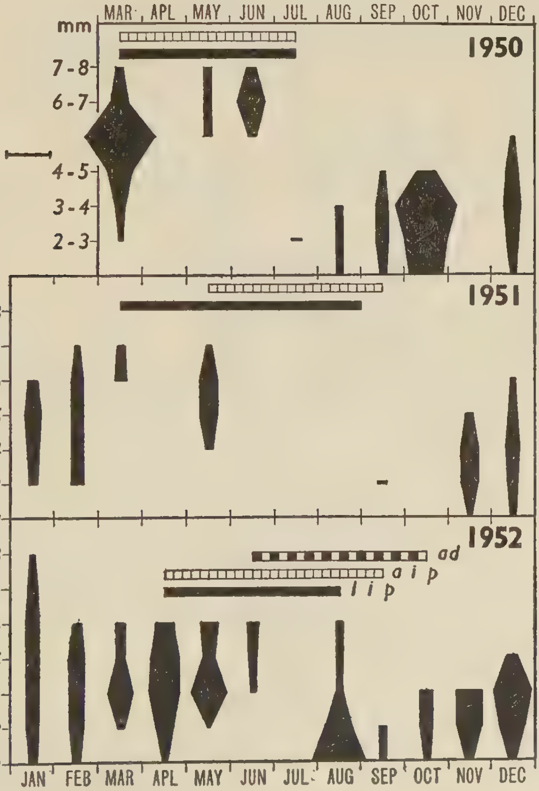

Fig. 1.—*Agapetus fuscipes*. Numbers in different size groups in successive months. (*ad*, adults; *a i p*, adults in pupal cases; *l i p*, larvae in pupal cases. Scale line, 50 larvae.)

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just below station 4. The collecting station (*Ss*) is some 100 m. above the confluence, and the stream is dry during periods of drought. Outgate is the second tributary and has a slower flow than Sykeside. The station (*Og*) is not far below the bog in which the stream rises. A full description of the stream is given by Macan (1957), who has also described the collecting methods (1958).

Stations 1, 2, 3 in the main stream and *Ss* and *Og* were visited monthly for three years and collections were made with a pond net for a period of ten minutes. Station 4 was visited monthly for one year only. In 1952 a cage to catch the emerging adults was placed near station 1 and was visited as often as necessary during the emergence period. The collections were sorted while the animals were alive, and all but the Ephemeroptera were preserved. It is on this preserved material that the paper is based. The main object of the investigation was a study of the Ephemeroptera. Had it been primarily a study of the Trichoptera, a collecting period of longer than ten minutes would have been desirable because members of this group were less numerous than those of the Ephemeroptera.

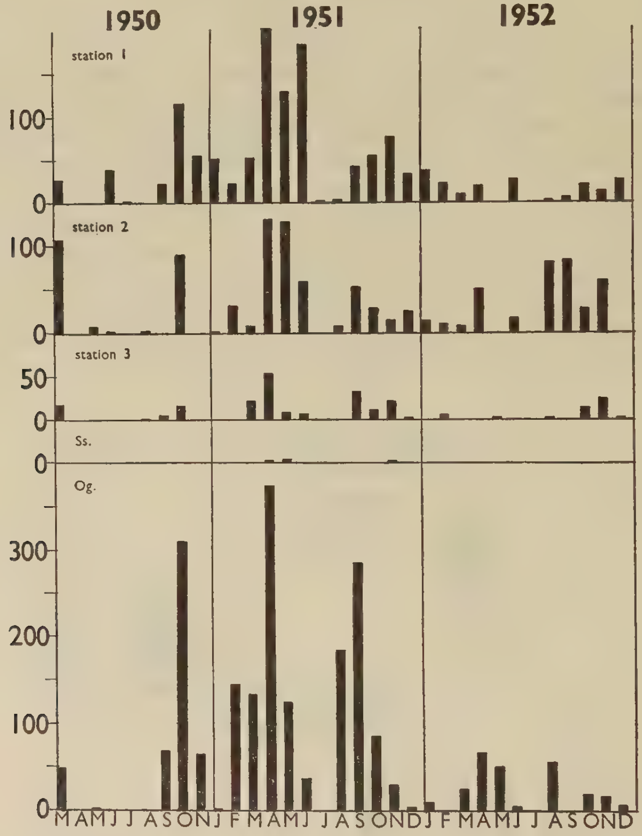

Fig. 2.—*Agapetus fuscipes.* Numbers at five stations in successive months.

Much taxonomic work, which necessitated the breeding of undescribed larvae to obtain known adults and the finding of differences between them, was necessary before any larvae could be named reliably. All the British species in three genera were obtained, and they have been described (Mackereth, 1954 ; 1957). In some of the others, differences were found only between the species recorded from the district. Even this was not always achieved and, owing to the large number of species, it proved impossible to reach a stage where trustworthy names could be applied to larvae in the family Limnephilidae. Miss R. M. Badcock, who is studying the genus, kindly named the specimens of *Hydropsyche.*

Fifteen species were found in the stream, excluding the limnephilids. They are listed below in order of abundance with the total number of larvae (*l*) and pupae (*p*) taken in the three years, first the cased then the uncased species.

Agapetus fuscipes Curt., 4593 *l.*, 411 *p.*
Silo pallipes F., 334 *l.*, 143 *p.*
Sericostoma personatum Spence, 42 *l.*, 1 *p.*
Odontocerum albicorne Scop., 37 *l.*
Glossosoma boltoni Curt,. 23 *l.*, 4 *p.*
G. vernale Pict., 1 *l.*
Crunoecia irrorata Curt., 1 *l.*
Limnephilids 464 + *l.*, 15 *p.*
Plectrocnemia conspersa Curt., 374 *l.*, 13 *p.*
Wormaldia occipitalis Pict., 369 *l.*, 2 *p.*
Hydropsyche instabilis Curt., 94 *l.*
Diplectrona felix McLach., 76 *l.*
Rhyacophila dorsalis Curt., 72 *l.*, 21 *p.*
Hydropsyche fulvipes Curt., 63 *l.*
Rhyacophila obliterata McLach., 17 *l.*
Philapotamus montanus Don., 10 *l.*, 1 *p.*

LIFE HISTORIES AND DISTRIBUTION OF CASED LARVAE

Agapetus fuscipes, the most abundant species in the stream, has an emergence period from early summer to autumn, and completes a generation in a year (fig. 1).

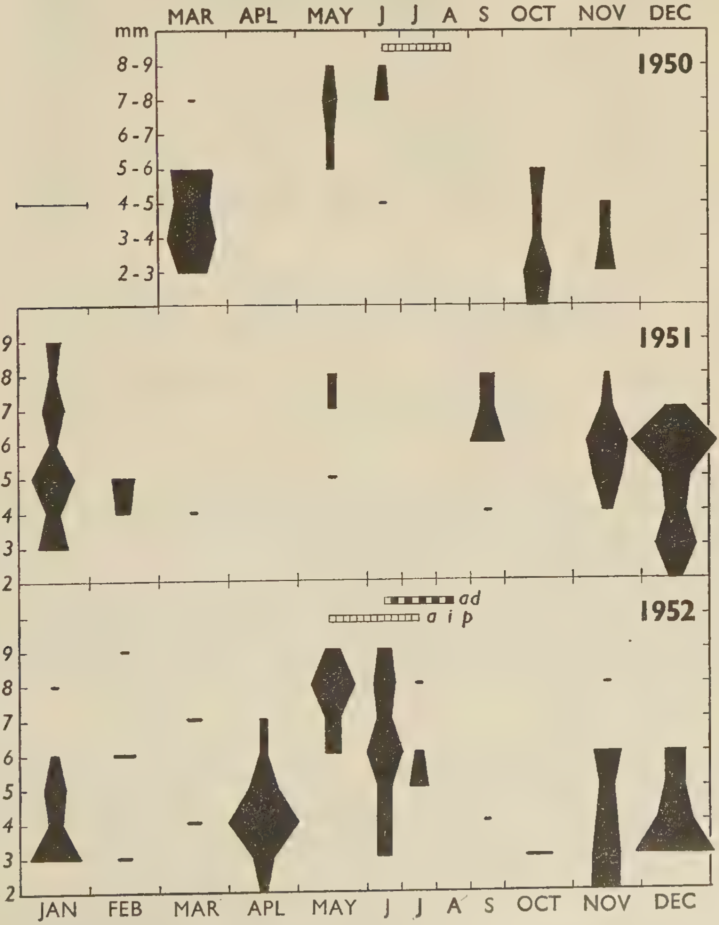

FIG. 3.—*Silo pallipes.* Numbers in different size groups in successive months. (*ad*, adults; *a i p*, adults in pupal cases. Scale line, 10 larvae.)

In the 1950–51 growth period there seemed to be a steady growth throughout the winter, and no larvae in the 1–2 mm. size group were found after December. In the 1951–52 season there appeared to be little or no growth in the winter months and 1–2 mm. larvae were found until April. The reason was not apparent. Figure 2 shows the distribution at the five stations throughout the three years. Outgate was found to be most densely populated, and fair numbers were taken at stations 1 and 2. Sykeside and station 3 were thinly populated, and no specimens were taken at station 4. During the 1950–51 season many more larvae were collected than in the 1951–52 season; a careful check (Macan, 1957 : 321) showed that this was not due to over-collecting.

Silo pallipes also has a one-year life cycle (fig. 3). The pupation and flight period were short compared with the previous species. Pupae were found for three months only in the two seasons. The time lag of one month between pupae and adults indicates that this species spends about one month as a pupa. Figure 4 shows the distribution of *Silo pallipes*. Station 1 was the most populated, Outgate the least. The Ichneumon fly, *Agriotypus armatus* Curtis, was found parasitising *Silo*; an average of one each month was found in 1952.

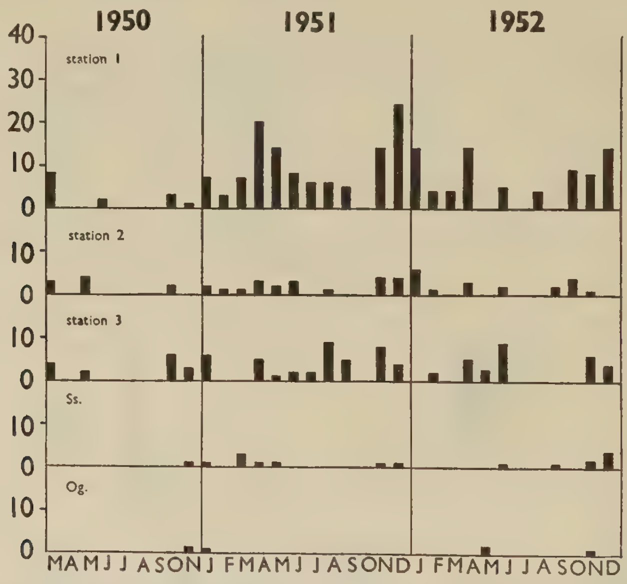

Fig. 4.—*Silo pallipes.* Numbers at five stations in successive months.

Sericostoma personatum, *Odontocerum albicorne* and *Glossosoma boltoni*, all rather scarce, were found in the main stream only. Unidentified limnephilids were sparse in the main stream, but were collected in large numbers from Sykeside in certain months. Station 4 was very poorly populated with cased caddis and only odd specimens were found there.

Life Histories and Distribution of Larvae without Cases

Hydropsyche instabilis, *H. fulvipes* and *Diplectrona felix* were found only in the main stream. The figures below show the percentage of each species at each of the stations where any of them occurred.

	St. 1	St. 2	St. 3	St. 4
H. fulvipes	56%	42%	34%	.
H. instabilis	44%	49%	52%	2%
D. felix		9%	14%	98%

H. fulvipes was most common at station 1., *H. instabilis* at station 3 and *D. felix* at station 4.

Plectrocnemia conspersa specimens were found in all size groups every month and therefore it was not possible to determine the life history. Pupae were found in May at one station, and adults have been collected in September, which could indicate a four to five month egg-laying period. Figure 5 shows that the numbers increased upstream, particularly at Sykeside and Outgate where Hydropsychids were absent. Station 4 is not shown in the figure, but many individuals of *P. conspersa* were taken there during the one year when collections were made.

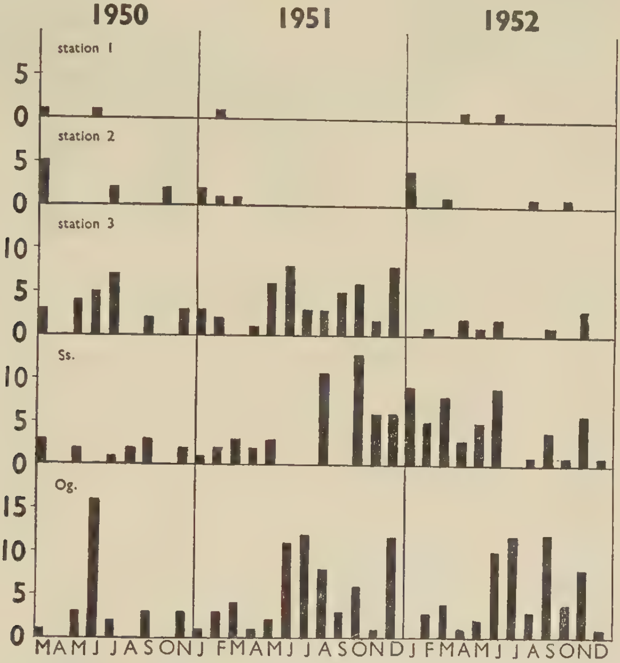

FIG. 5.—*Plectrocnemia conspersa.* Numbers at five stations in successive months.

Wormaldia occipitalis.—Figure 6 shows the total numbers in each size group of this insect for the 14 months starting November, 1951. May and July are omitted because ten minute collections were not made in those months. Half-grown larvae were found throughout the summer months, and fully grown larvae in the winter; the emergence period, a short one, was in the late summer. The data suggest a two-year life cycle; the larvae hatch in the late summer, and there is not much growth during the first winter; then there is growth throughout the following summer, and none during the second winter; pupation is in late spring and emergence starts in August. Most of the larvae were collected from Outgate (fig. 7) especially at the beginning of the third season.

Rhyacophila dorsalis was collected every month in small numbers, and there was a large range throughout the size groups. Emergence of the adults was from early spring until late autumn. In late October a quantity of what appeared to be pupae of this species were found in the River Brathay (*WL*). They were in fact larvae in the pupal cases and they overwintered in that state. Metamorphosis started in the early spring and finally the first emerged at the beginning of June. There are two possible explanations: they were the offspring of insects which had emerged early and which, after growing rapidly throughout the summer, spent the winter in the pupal case, or they were the offspring of insects emerging very late, which were unable to reach the pupal stage during the summer and therefore had to spend a second winter as larvae but this time in the pupal case.

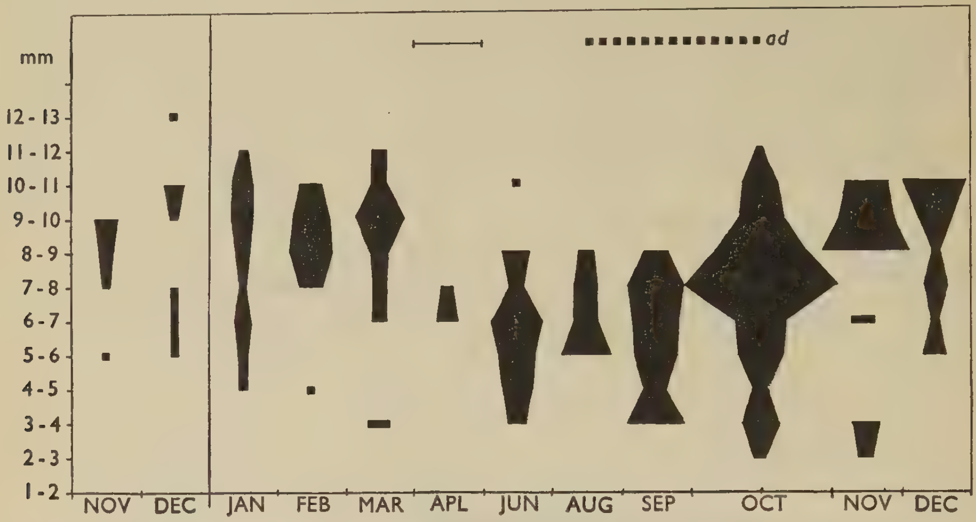

FIG. 6.—*Wormaldia occipitalis.* Numbers in different size groups in successive months. (*ad*, adults. Scale line, 10 larvae.)

R. obliterata emerges in autumn. The few specimens taken were mainly from station 1.

TABLE I.—*Occurrence of the species at the six stations*

(*X* abundant, + present, *o* not found)

Cased larvae:	St. 1	St. 2	St. 3	St. 4	*Ss*	*Og*
Agapetus fuscipes	+	+	+	*o*	+	*X*
Silo pallipes	*X*	+	+	1	+	+
Sericostoma personatum	+	+	+	*o*	*o*	*o*
Odontocerum albicorne	+	+	+	*o*	*o*	*o*
Glossosoma boltoni	+	+	+	*o*	*o*	*o*
G. vernale	1	*o*	*o*	*o*	*o*	*o*
Crunoecia irrorata	1	*o*	*o*	*o*	*o*	*o*
Uncased larvae:						
Plectrocnemia conspersa	+	+	+	*X*	*X*	*X*
Wormaldia occipitalis	+	+	+	*o*	+	*X*
Hydropsyche fulvipes	*X*	+	+	*o*	*o*	*o*
H. instabilis	+	+	*X*	*o*	*o*	*o*
Diplectrona felix	*o*	+	+	*X*	*o*	*o*
Rhyacophila dorsalis	*X*	*X*	*X*	*o*	+	1
R. obliterata	+	+	1	*o*	*o*	*o*
Philapotamus montanus	+	*o*	1	*o*	*o*	*o*

The population of the lower part of the main beck (stations 1, 2 and 3) is fairly uniform, but becomes distinctly sparser higher up, only six of the 15 species being found at station 4, *Ss* and *Og*. This is a bigger difference than was noticed in the Plecoptera by Mackereth (1957) or in the Ephemeroptera by Macan (1957). Nearly all the specimens of *Diplectrona felix* were taken at station 4, *Plectrocnemia conspersa* was more abundant at all three of the higher stations than lower down, and *Wormaldia occipitalis*, a third net-spinner, was markedly more abundant at *Og* than elsewhere. This pattern is unlike that shown by either of the other two orders mentioned.

Comparison with other streams is not thought to be worth while because all other lists of species known to the writer are based on adults which had been bred. Clearly only a small proportion of larvae collected can be bred out and this method cannot give a complete picture.

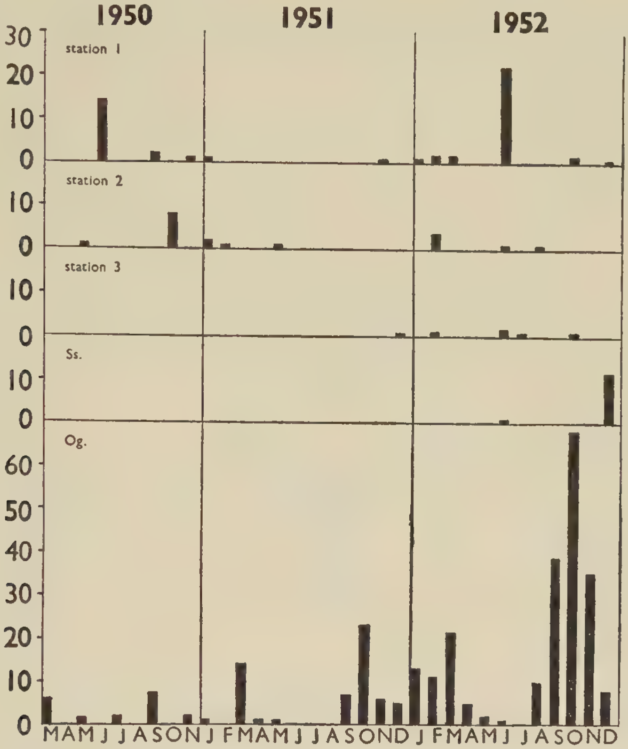

FIG. 7.—*Wormaldia occipitalis.* Numbers at five stations in successive months.

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I wish to express my thanks to Dr. T. T. Macan for his guidance and advice throughout this work, and to Miss R. M. Badcock for identifying the *Hydropsyche.*

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THE RECOGNITION OF THE IMMATURE STAGES OF *ELACHIPTERA CORNUTA* (FALLÉN) (DIPTERA : CHLOROPIDAE), WITH NOTES ON ITS ASSOCIATION WITH *OSCINELLA FRIT* (L.) IN OATFIELDS

By W. F. Jepson and T. R. E. Southwood
(Imperial College, London)

In the course of ecological studies on populations of *Oscinella frit* (L.) in oatfields and grass headlands we have been puzzled by an upswing in the numbers of eggs found in soil samples, taken with the Cardiff grab sampler (Webley, 1957), during the second and third weeks of June, by which time the spring oviposition of *O. frit* should be on the wane. In 1958, these late eggs were particularly abundant and, although individually they closely resembled those of *O. frit*, when larger groups were compared, certain differences could be noted.

These eggs were hatched out and proved to be those of the Chloropid *Elachiptera cornuta* Fallén. This species is well known as a follower of *Oscinella frit* in infested cereal fields, and, according to Mesnil (1935), who has summarised the scattered references to the insect, *E. cornuta* larvae are exclusively detritus feeders. Goodliffe (1942) bred both *E. cornuta* and *Lasiosina cinctipes* (Meigen) from barley plants infested with *Chlorops pumilionis* (Bjerkander), the gout fly. Walton (1937), however, drew attention to the fact that many of the larvae found by him in Gloucestershire in June, 1936 were in plants which showed no signs of an infestation by *O. frit*.

As a result of this discovery we consider that there may well be some risk of overestimation of numbers of *O. frit* if careful attention is not paid to the identification of the eggs and larvae found in surveys. The present paper attempts to give the characters by which the immature stages of *E. cornuta*, which were not described by Nye (1958), can be distinguished from those of *O. frit*. Further, the first instar larvae of Oscinellines have not hitherto been described in detail. Some biological notes are given on the occurrence of *E. cornuta* in oatfields.

Comparison of the Immature Stages of Elachiptera cornuta *with those of* Oscinella frit

Eggs

It is not always possible to be certain of distinguishing isolated eggs of these species, but when groups of five or six of each can be seen together, the following characteristics may be helpful.

E. cornuta (Fig. 1*D*) Length 0·5–0·8 mm.	*O. frit* (Fig. 1*E*) Length 0·6–0·8 mm.
Striations rather coarser and micropylar area centrally placed on bluntly rounded apex.	Striated and sculptured, with terminal micropylar area on asymmetrically tapered apex.
Form of egg more broadly cigar-shaped.	Form of egg slightly sickle- or crescent-shaped.

The extreme forms are shown in figure 1, but often the diagnostic characters are not so distinct and identification must be confirmed by an examination of the

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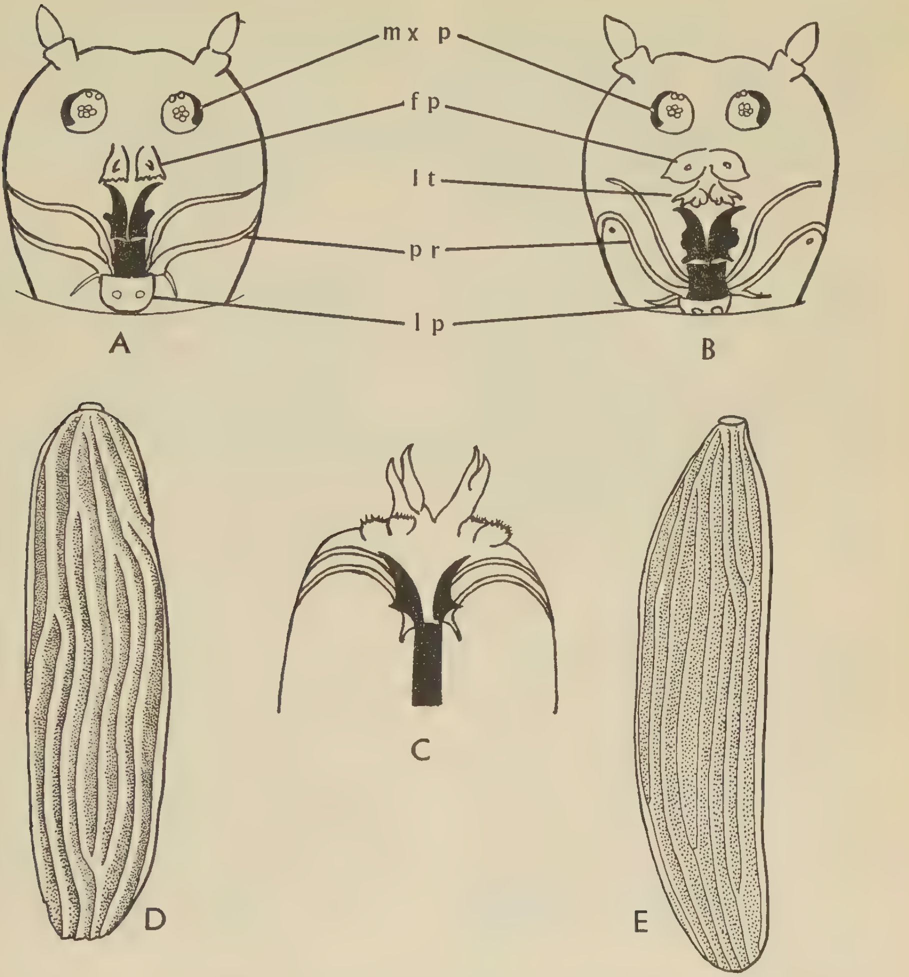

FIG. 1.—Ventral views of heads of newly-hatched larvae: (*A*) *Elachiptera cornuta* (Fallén): (*B*) *Oscinella frit* (L.); (*C*) *E. cornuta* showing everted mouth hooks; (*D–E*) eggs, extreme forms: (*D*) *E. cornuta*; (*E*) *O. frit.* (*fp*, frontal palp; *lp*, labial palp; *lt*, labral teeth; *mxp*, maxillary palp; *pr*, perioral ramus.)

larvae. If the eggs are allowed to remain in tap water at laboratory temperatures they will hatch in three to four days and the young larvae will live up to ten days or more in this state.

First Instar Larvae

These are superficially identical; slender, transparent and metapneustic, the posterior spiracles bearing the four-branched processes typical of the Oscinelline larvae. They are on an average 1·2 mm. long.

The larvae are most easily examined alive after mounting in a drop of soda water or 10 per cent. ethyl carbamate solution, which immobilises them, or they may be killed without any contraction by gently heating the slide. The main characters, visible only with some difficulty under high power magnification, are tabulated below; several of these will serve to distinguish the two species.

E. cornuta	*O. frit*
Head and facial mask : Fig. 1*A* and *C*.	Fig. 1*B*.
Antennae : 2-segmented.	2-segmented.
Maxillary palp : two anterior and about five central sensillae ; small arcuate sclerite anteriorly.	indistinguishable from *E. cornuta*.
Frontal palp : (" Biscuit-shaped organ " of Nartshuk, 1956) : rounded quadrate plates, posterior border toothed and ciliated or minutely setose, slightly bilobed ; central " sensilla ".	suboval, transverse, slightly pointed postero-laterally ; central " sensilla ".
Labral teeth : normally retracted under frontal palp ; when extruded seen as four fleshy teeth (fig. 1*C*).	tips always visible, slightly sclerotised ; a pair of spines exteriorly and a pair of rounded cusps interiorly on each side (fig. 1*B*).
Mouth hooks : more slender ; sickle-like, with one distinct accessory cusp.	stouter, with two accessory cusps and a basal cusp.
Perioral rami : two rami issue from hypostomal region and run almost laterally, finally tending to converge at the side of the head and form a distinct crescentic cell on the face. From root of hind ramus runs a small backwardly-pointing ramal spur.	two rami issue from hypostomal region and run forward and curve outwards over the face. Anterior ramus ends laterally, posterior ramus turns back and forms an almost closed oval cell in which is a sensilla. Posteriorly to insertion of main ramus at oral margin is a small laterally directed ramus on each side.
(This is the main diagnostic feature for an experienced observer.)	
Thoracic and Abdominal Ventral Spicule Bands	
Thoracic I : many broken rows (7–8) of uniform small, rounded close-set spicules.	indistinguishable from *E. cornuta*.
Thoracic II and III : no spicules.	indistinguishable from *E. cornuta*.
Abdominal I : (fig. 2*A*) : more reduced than in *O. frit* ; usually three rows, close together, and unbowed, middle row stouter ; sometimes reduced to two rows.	(fig. 2*B*) : patterned as for other abdominal segments but reduced to four rows, anterior rows markedly bowed, median rows of rather stouter blunt spicules.
Abdomen 2–8 : (fig. 2*C*) highly developed crawling pads visible laterally as ventral swellings with eight transverse rows of spicules forming an elliptical closed figure on each segment. The two outer rows, 1 and 8, of uniform small rounded spicules ; rows 2, 3 and 4 of slightly larger spicules, row 4 being slightly fragmented ; rows 5 and 6 of still larger rounded, occasionally pointed, spicules ; row 7 with much larger, generally rounded or blunt, almost square-edged spicules.	(fig. 2*D*) very similar pads to those of *E. cornuta* but rows 3 and 4 more reduced ; the spicules of row 6 larger than those in *E. cornuta*, whilst those of row 7 are slightly smaller.
Pre-anal : single row of less than a dozen small rounded spicules; no post-anal row.	indistinguishable from *E. cornuta*.

As the eight-row pad appears to occur in the first instar larvae of most Oscinellinae it would seem that it could be regarded as the more primitive condition in the group and that the single spicule rows found in the third instar larvae of *O. frit* are vestigial. We may, therefore, conveniently follow the nomenclature of Mesnil (1935) and Nartshuk (1956). The eight-row pad of the first instar of *E. cornuta* and *Oscinella* then becomes :

Anterior row (1)	1
Intercalary rows (2, 3, 4)	3
Median rows (5, 6)	2
Main row (7)	1
Posterior row (8)	1

Second Instar Larvae

There is less danger of confusion of the species in the second and third instars. The facial mask of *O. frit* in the second instar is figured by Mesnil (1935) and, apart from the retention of the conspicuous labral teeth, it resembles that of the third instar described by Jepson and Nye (1957) and Nye (1958) with unserrated perioral rami. On the other hand, the facial mask of *E. cornuta* becomes more complex, with six serrated perioral rami on each side. Both larvae become amphipneustic, the number of spiracular digitations varying from 5–7.

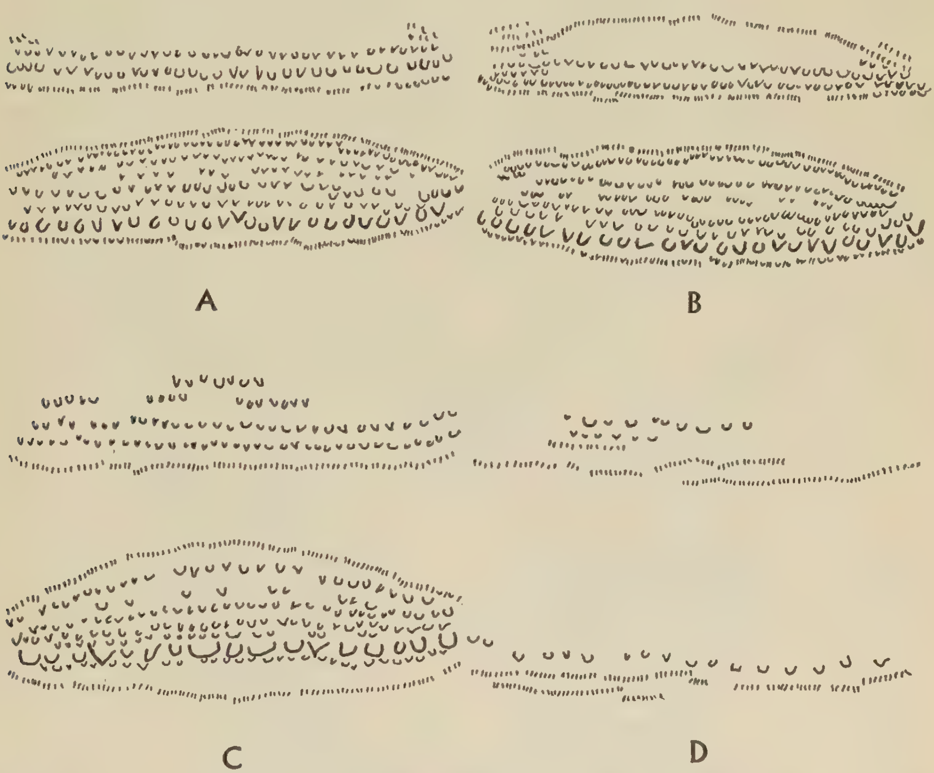

FIG. 2.—Diagrams of crawling pad spicules of first and second abdominal segments : (*A*) *Elachiptera cornuta* (Fallén), first instar larva ; (*B*) *Oscinella frit* (L.), ditto ; (*C*) *E. cornuta*, second instar larva ; (*D*) *O. frit*, ditto.

The ventral spicules also show greater divergence than in the first instar. In *O. frit* the complex crawling pads on abdominal segments 2–8 are reduced to two rows, the anterior of which consists of slightly enlarged sparser spicules. In *E. cornuta* the eight rows of spicules are even more strongly developed than in the first instar, those of the sixth being markedly stouter than the rest.

Third Instar Larvae

The distinction between larvae of the *Oscinella* species complex which are likely to occur in oats, and those of *E. cornuta*, in the third instar, presents little difficulty. It is sufficient to compare the facial masks. In *O. frit* the mask is simple and consists of a closed polygonal cell, the frontal palp, on each side, with a number of perioral rami running longitudinally backwards to the mouth opening and divided by cross rami into a maximum of eight closed cells on each side (Jepson and Nye, 1957 ;

Nye 1958). In *E. cornuta* (fig. 3), on the other hand, the mask consists of two distinct areas of rami. Anteriorly, and extending nearly to the maxillary palp areas, there are about seven broken, wavy rows of shortly fringed rami. Behind the level of the mouth hooks and laterally on the face run 12 double rows of rather heavily serrated or shortly fringed rami, which arch back and end at the margin of the head.

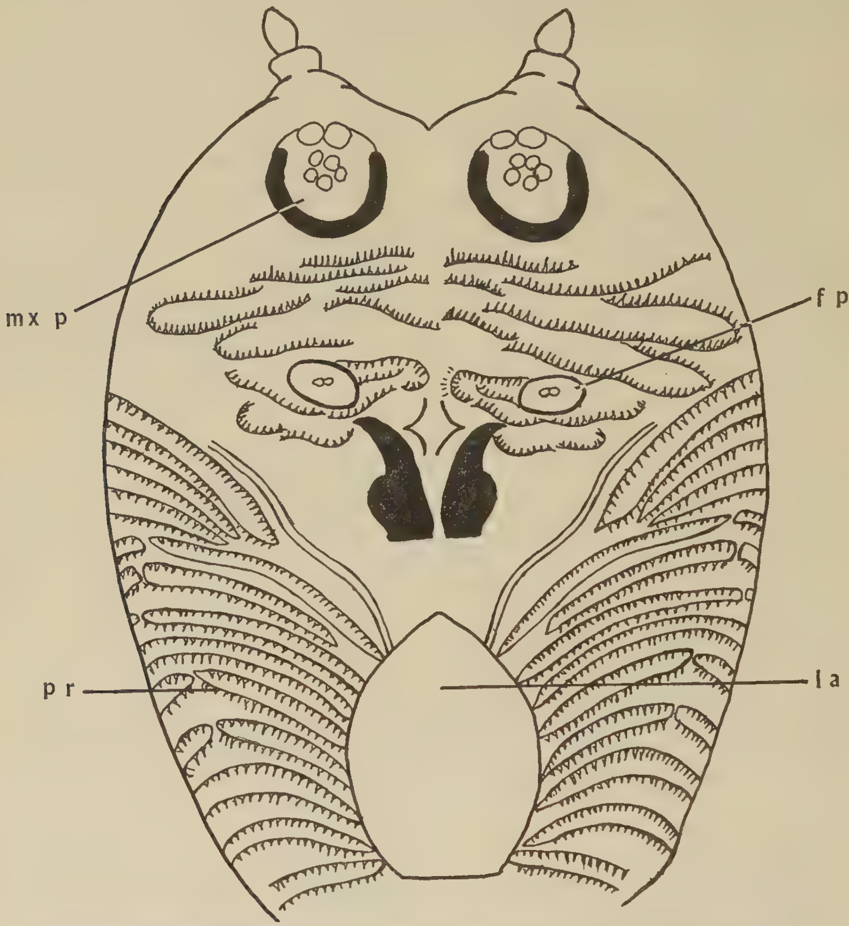

Fig. 3.—*Elachiptera cornuta* (Fallén), third instar larva, ventral view of facial mask. (*fp*, frontal palp ; *la*, labral plate ; *mx p*, maxillary palp ; *pr*, perioral rami.)

Other differences are : the presence of at least two to three rows of small uniform spicules on thoracic segments II and III of *O. frit*, those of *E. cornuta* remaining bare ; the reduction of the eight-row crawling pad in *O. frit* (fig. 2*D*) to single rows of small rounded spicules on abdominal segments 2–8, compared with the retention of the full eight-row pad in *E. cornuta* (fig. 2*C*) and the wider separation of the posterior spiracular lobes in *E. cornuta*. The two latter characters also persist and serve to identify the puparia.

Notes on the Biology of Elachiptera cornuta *in Oatfields*

In past years, the adult of *E. cornuta* has been taken very early in the season, *e.g.* 16th April, 1956, and this may be due to the habit, recorded by Mesnil (1935), of hibernating in dead stems. The numbers caught have never been more than isolated individuals and they are certainly never swept in large numbers over spring oats at this time. It is probable that the large numbers of eggs found in mid-June are laid by an invasion of flies from the grass headlands into fields containing many oat stems damaged by *O. frit.*

Mature larvae of this generation of *E. cornuta* were found in exceptional abundance in 1958 in late samples of oat shoots taken up to the time of emergence of the tiller generation of *O. frit.* The adults of the new *E. cornuta* generation attained peak numbers on 3rd July, when there were 4·6 per square yard, compared with 5·5 per square yard for *O. frit*—estimated from samples taken by the tent method (Jepson and Southwood, 1958). *E. cornuta* was much less frequently taken by sweeping. A second generation was detected at the end of August at the same time as the peak of the panicle generation of *O. frit*, 28th August ; the numbers of *E. cornuta* were about equal to those in early July, although the *O. frit* were much more numerous. These flies are thought to lay their eggs under debris of fallen plants and even under bark, and presumably develop slowly in the decaying matter. According to Mesnil (1935), some hibernate in groups of several hundred strong huddled together, as does *Chloropisca glabra* (Meigen). However, Professor O. W. Richards has kindly provided us with his records (25 in all) of *E. cornuta* ; he has taken specimens as early as 3rd March and as late as 26th October, and in all the summer months, but never during the winter.

The detection of *E. cornuta* eggs in surveys of *O. frit* will be simplified if any sudden increase in egg numbers after 5th or 6th June in a normal year, that has followed an adult peak of *O. frit* around 25th May, is treated with suspicion, and all samples examined carefully, as suggested above. If any counts are made of larvae in the shoots of an infected crop of spring oats after the first week in June, care should be taken as a large proportion of these can be *E. cornuta.*

ACKNOWLEDGMENTS

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FURTHER EFFECTS OF *LASIUS NIGER* L. ON *APHIS FABAE* SCOPOLI

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Introduction

Recent experimental work has borne out the claim made originally by Herzig (1937) that *L. niger* collecting honeydew from *A. fabae* causes the aphids to multiply faster, and does so partly by some means more direct than merely preventing contamination of the aphids by honeydew and moulds or protecting them from their enemies. Way (1954) first obtained experimental evidence of such an effect of an ant upon its honeydew provider, in the case of *Oecophylla longinoda* Latr. and the coccid *Saissetia zanzibarensis* Williams. El-Ziady and Kennedy (1956) confirmed that *L. niger* accelerates the multiplication of *A. fabae*, and showed also that the ants retard the transition from production of apterae to that of alatae in crowded colonies. Banks (1958), working with the same two species, again confirmed the acceleration of aphid multiplication, and gave evidence that one way in which the ants bring this about is indirect: by retarding the dispersal of the young adult aphids from the growing point of the plant where larviposition is most rapid. Banks and Nixon (1958) went on to confirm by radio-tracer that *L. niger* stimulates *A. fabae* to feed faster as Herzig had claimed, but still doubted whether ant-attendance had any direct effect on the aphids' nutrition and rate of larviposition. The direct effects of stimulation by *L. niger* on the growth, development and larviposition of *A. fabae* were examined in the present work.

Materials and Methods

The experiments were done between mid-June and September, 1956, in a screened glasshouse where *Lasius niger* was active in the absence of aphid parasites and predators. The temperature was maintained thermostatically and by hand-controlled ventilation to within a few degrees of 70° F. day and night, except for about seven days (mainly during the fourth and fifth experimental generations) when it rose to 75–80° F.

The experimental aphids were derived from the stock clonal culture described by Kennedy and Booth (1954). Twenty to thirty adult apterae were transferred to each of ten similar potted plants of *Vicia faba* var. Seville Longpod, and removed the next day. The plants bearing the young were then installed in the greenhouse, five accessible to ants and five isolated over an oil tray. These young formed the first generation of the experimental series.

In this work, as opposed to the previous experiments of El-Ziady and Kennedy (1956) and of Banks (1958), the shoot tips with the growing leaves were cut off every plant before use. This served to minimise any indirect effects of the ants through their influence on the distribution of the aphids among leaves of unequal suitability (Banks, 1958) and facilitated counting of the aphids. Presumably as a result of the relative unsuitability of the only leaves thus provided for aphid colonisation, the young apterous adults settled down less readily on the plants than they had in the earlier work and showed a tendency to produce more alate offspring. To reduce losses of adults, the pots were stood in water trays, with a small wooden bridge from each

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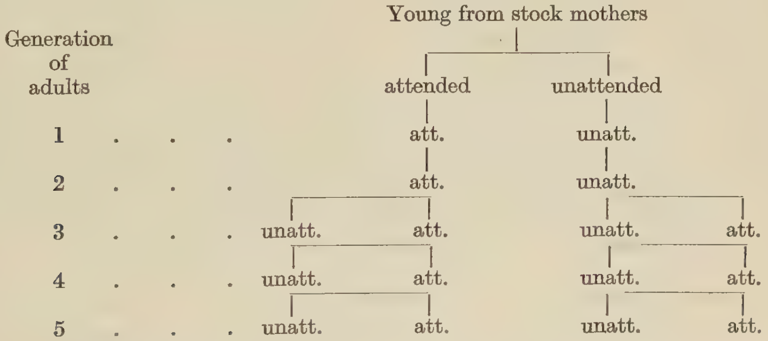
ant-attended pot to the bench, which the ants but not the aphids quickly found and used. Aphids found wandering on the soil or pot were replaced on each plant once a day, but some walked right off and were drowned.

All the plants were examined at least once daily and records kept of the duration of development from birth to adult, of the weights and initial larviposition rates of the young apterous adults, and of the rates of departure and total young deposited by the apterous adults of each generation, with daily removal and recording of the form of any new adults to prevent a third generation developing on the plants. Not all these items could be recorded in every treatment of every generation.

Each generation of new apterous adults was subcultured on a new batch of plants. The alate adults were discarded after being counted. The successive cultures, after the first, were started with 30 newly-moulted adult apterae transferred to each of five plants for each treatment. For some of the measurements in the third generation, similar adults were transferred to a second, duplicate set of five plants a day or two after the first set were infested. The adults were taken from among the first to appear in the progeny of the previous generation, with a day or two's delay where necessary to ensure synchronisation of the generations under the different treatments. Sister adults were transferred concurrently to parallel sets of five plants but removed again after 24 hours' larviposition, and these young were used to measure the duration of development under each treatment in each generation.

Thus the young of each generation developed from birth to adulthood under the same treatment, ant-attended or ant-free, as their adult mothers. Subculturing was continued for five generations in two main lineages, one continuously attended by ants and the other continuously ant-free, plus off-shoot sister cultures given the opposite treatment in the third to fifth generation, thus :



This procedure permitted comparisons to be made between aphids developing under the same external conditions on plants from the same batch, but differing in being attended or unattended by ants both currently, and in previous generations up to a maximum of four. Some of the new adults of the fourth generation of each main lineage were transferred to separate sets of plants (30 per plant) under the same treatments as before, but in this case the young were not left to develop with their mothers but were transferred as new-born larvae to new plants as described later.

RESULTS

Rate of development.—The minimum number of days taken by the apterae (alatae were not considered here) from birth to reaching the adult stage in each of four generations of the main lineages, is shown in Table I. This minimum period was in practice the time taken by the majority of young, for on the first day that any became adult, the majority did so (out of a total of 100–200 individuals per treatment batch). The developmental period was consistently shorter with ants currently in attendance, by 14–25 per cent.

Table I.—*Duration of development (days) with and without continuous attendance by ants. Means and S.D.s from* 5 *plants each in generations* 2, 4 *and* 5 *and from* 10 *plants in generation* 3

Treatment	Generation			
	2	3	4	5
Attended .	7±0	6·5±0·6	6±0	6±0
Unattended	8·2±0·5	8·3±0·5	7±0	8±0

The sister cultures of one of the duplicate batches of five plants of the third generation of each line were given the opposite treatment in order to test for maternal effects on the rate of development. Table II gives the time taken by the young apterae from birth to adult, in the four different treatments. Attendance of the mother during her own larval development hastened the post-natal development of her young, whether or not ant-attendance continued during their birth and development.

Table II.—*Duration of development (days) with and without ant-attendance in the current (third) and previous generation. Means and S.D.s from* 5 *plants*

	Mother's pre-adult treatment	
Current treatment	Attended	Unattended
Attended . .	5·5±0·6	7±0
Unattended . .	6·5±0·6	8±0

Rate of growth.—Thirty of the first-produced apterous adults taken at random from the five plants of each treatment were weighed individually before transfer to the new plants. Those from ant-attended cultures were consistently heavier than those from the unattended cultures, by 15–69 per cent. (Table III). The mean ratio of attended to unattended adult weight was significantly greater than one ($P<0{\cdot}01$). Weights at birth were not known but were very small compared with adult weights, so relative growth rates are estimated in Table III as new adult weights divided by the duration of development in days (Table I). Because the heavier ant-attended adults had reached that stage more quickly than the unattended, their estimated growth rates were 53–97 per cent. higher.

Table III.—*Mean weights of* 30 *new adults and their estimated mean growth rates as larvae, with and without continuous attendance by ants*

		Generation			
	Treatment	2	3	4	5
Weight, mg. .	Attended	0·913	0·778	0·711	0·974
	Unattended	0·540	0·643	0·453	0·846
Duration of development, days .	Attended	7±0	6·5±0·6	6±0	6±0
	Unattended	8·2±0·5	8·3±0·5	7±0	8±0
Growth rate, µg./day .	Attended	130	120	119	162
	Unattended	66	78	65	106

Initial rate of larviposition.—This was estimated as the number of larvae counted on each plant two days after the new adults had been transferred there, divided by the number of those adults (30±1) present on the first day. The mean rate of larviposition per plant was higher with ants than without them (insignificantly so in the fourth generation) in the three generations of the main lineages in which it was assessed (Table IV: compare lines 1 and 4). When ant-attendance ceased at the adult stage, the initial larviposition rate was lower (insignificantly so in the fourth generation) than when attendance continued (compare lines 1 and 2). *Vice versa*, when attendance began for the first time in the adult stage the rate was higher than when it did not (compare lines 3 and 4). Table IV shows no significant effect of attendance before the adult stage was reached, upon the initial larviposition rate (compare lines 1 and 3, and 2 and 4), except in the attended adults of the third generation.

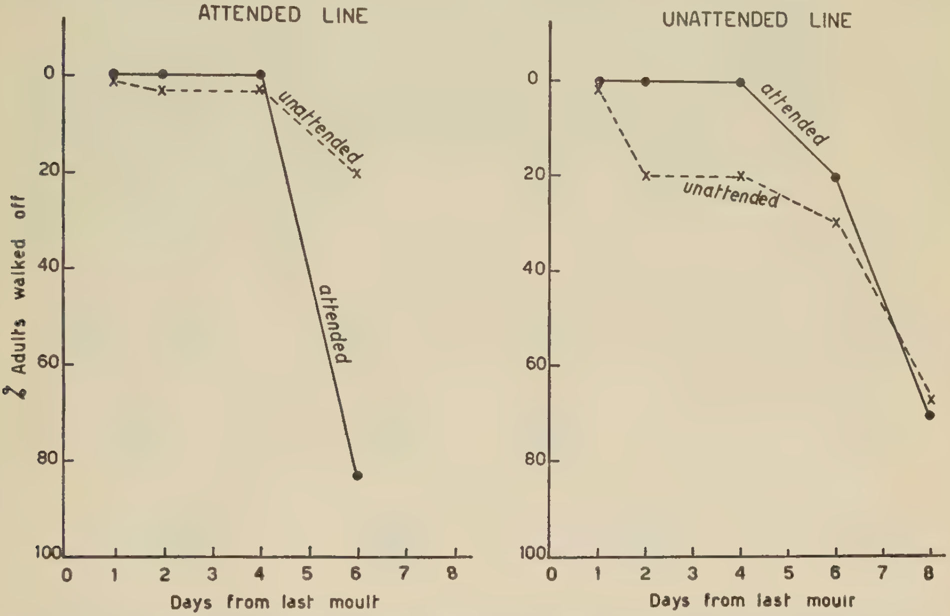


FIG. 1.—Emigration from plants by adult apterae of the third generation. *Left :* aphids attended by ants throughout the previous and present generations (*solid line*) compared with their sisters on which the ant-attendance ceased after the last moult (*broken line*). *Right :* aphids kept free of ants throughout the previous and present generations (*broken line*) compared with their sisters on which ant-attendance began after the last moult (*solid line*).

TABLE IV.—*Initial* (2-*day*) *larviposition rates with and without ant-attendance in the current and previous generations. Means and S.D.s from* 10 *plants in generation* 3 *and from* 5 *plants each in generations* 4 *and* 5

Previous treatment	Current treatment	Generation 3	Generation 4	Generation 5
Attended .	Attended	20±3	17±4	9±1
	Unattended	10±2	14±0	5±1
Unattended .	Attended	12±3	18±4	6±4
	Unattended	7±2	15±1	4±1

Wandering of adults.—During the first day or two after transfer to new plants the attended adults wandered no more, and on the whole rather less, than the unattended adults. As the young they were depositing accumulated, however, the attended adults became noticeably more restless than the unattended. Table V shows that the attended adults wandered off the plants more than the unattended adults in the second to fifth generations of the main lines. Figures 1 and 2 show the detailed course of events in the third and fourth generations, comparing sister cultures of the same parentage. In each case the attended adults wandered off less, or no more, than the unattended at first, but after a few days of faster larviposition the attended adults left in larger numbers.

Table V.—*Percentages of apterous mothers that had departed from the plants* 6 *days after transfer, with and without continuous attendance by ants. Means and S.D.s from* 5 *plants each in generations* 2, 4 *and* 5 *and from* 10 *plants in generation* 3

	Generation			
Treatment	2	3	4	5
Attended .	55±4	83±9	40±6	55±12
Unattended .	21±2	37±9	31±11	12±3

This restlessness of attended adults in the presence of their young appeared to be connected with a change in the excretory behaviour which was observed in aphids attended by ants, as described previously by Banks (1958) for *A. fabae* and by Mittler (1958) for *Tuberolachnus salignus* Gmelin. Palpation by an ant had two distinct effects on the excretory activity of an aphid: first an excitatory one, eliciting immediate extrusion of a honeydew droplet (this response was re-elicitable only after an interval presumably spent in re-filling the rectum); and secondly an inhibitory effect which persisted between palpations. The normal, unattended, excretory performance of lifting the abdomen high off the plant, waving the legs and projecting the droplet through the air, was suppressed. Instead, a droplet was extruded only on palpation by the attendant ant, and retracted again into the rectum if it was not promptly removed by the ant. Close observation showed that attendant ants removed virtually every droplet the first time it was extruded by new adults which had produced no or few young, and by older adults which had moved away from the cluster of young and settled to feed elsewhere on the plant, and such adults were usually found at the same spot on successive days. But when an adult was surrounded by a number of young, the palpating ant often moved straight on after palpating it to the adjacent young without waiting to remove the droplet it stimulated the adult to extrude. The ant being then kept busy for a while collecting the smaller but more frequently produced droplets of the young, the adult aphid retracted its droplet and held it within the rectum until the ant eventually returned and palpated again. The greater restlessness of the attended

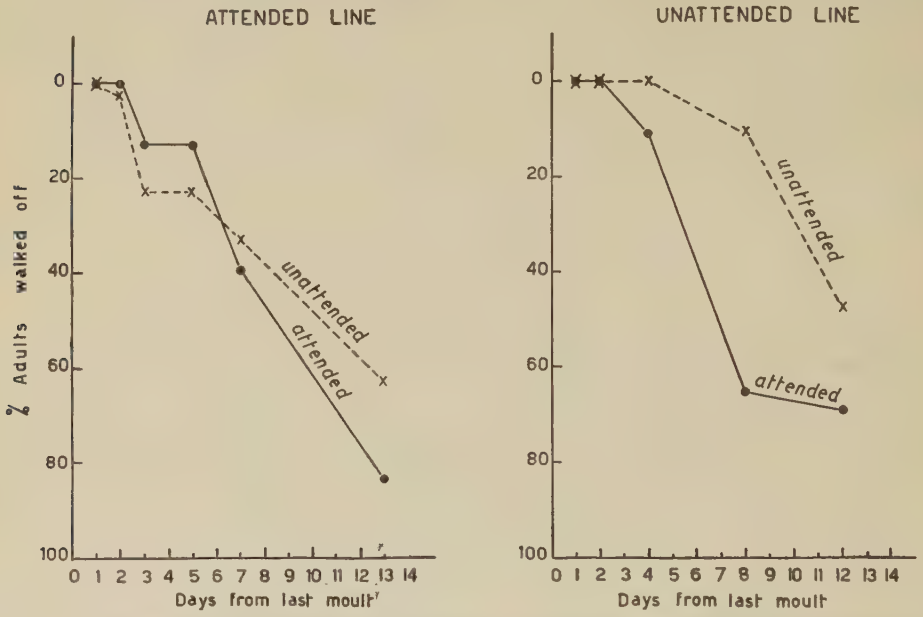


Fig. 2.—Emigration from plants by adult apterae of the fourth generation; otherwise as figure 1.

adults compared with the unattended, developed in the cultures when the attended adults came to be "neglected" in this way owing to the accumulation of young around them, while still being palpated often enough to be prevented from voiding their honeydew as the unattended adults did.

Total young deposited.—The adults that remained on the plants ceased larviposition after 24–30 days and died a few days later. These periods were not obviously affected by the ants. Comparing first the main lineages (lines 1 and 4 in Table VI), more young were deposited on the attended plants in every generation. In the sister cultures where ant-attendance had ceased before larviposition began, fewer young were deposited in the third and fourth generations but not in the fifth (compare lines 1 and 2 in Table VI). Where ant-attendance had begun for the first time at the adult stage, more young were always deposited than in the sister cultures which continued unattended (lines 3 and 4). Since the average mother stayed for a shorter time on the attended than on the unattended plants (above), it is evident that the larviposition rate of the attended adults was considerably higher than that of the unattended.

TABLE VI.—*Total young deposited per original mother settled on each plant, with and without attendant ants in the current and previous generations. Means and S.D.s from 5 plants*

Previous treatment	Current treatment	Generation			
		2	3	4	5
Attended	Attended	55±4	41±9	37±5	60±2
	Unattended	.	32±5	25±1	64±15
Unattended	Attended	.	50±15	38±6	63±10
	Unattended	32±5	30±9	28±4	48±15

Form of young.—The form of the young deposited by the mother apterae was recorded as the young became adult in the second to fourth generations (Table VII). Unattended mothers produced more winged offspring than attended mothers, whether or not the mothers had been attended before they became adult. There was no consistent effect of the pre-adult treatment of the mothers. Attendance during the immature stages reduced the proportion of winged young born to attended mothers in generations 2 and 3 but had the opposite effect in generation 4.

TABLE VII.—*Per cent. alate aphids produced on the plants, with and without attendant ants in the current and previous generations. Means and S.D.s from 5 plants*

Previous treatment	Current treatment	Generation		
		2	3	4
Attended	Attended	42±8	16±3	23±4
	Unattended	76±8	82±2	75±1
Unattended	Attended	62±6	24±1	11±1
	Unattended	73±8	79±5	.

Further separation of effects on mothers and daughters.—In the main experiment, above, the daughter aphids always received the same treatment as their adult mothers, at least until the daughters became adult. The daughters belonging to the fifth generation which were transferred to new plants at birth as mentioned under Methods served to eliminate any possible complication due to the presence of the mothers. Larvae born on the same day in each of the main lineages were distributed among ten plants (about 50 per plant), five plants being left attended and five unattended throughout the larval and adult life of this generation. This was repeated with three successive batches of larvae from the same mothers and the means (calculated as for previous Tables) from the 15 plants thus making up each of the four mother/daughter treatment groups are summarised in Table VIII.

TABLE VIII.—*Development, growth and larviposition with and without attendant ants throughout the previous and current generation. Means and S.D.s from* 15 *plants in each case*

Mothers' treatment:	Attended		Unattended	
Daughters' treatment:	Att.	Unatt.	Att.	Unatt.
Mean weight of new adults, mg.	0·903	0·974	1·029	0·860
Days from birth to adult	7·0±0·9	8·5±0·5	7·0±0·7	7·8±0·4
Mean growth rate to adult, µg./day	128	115	147	110
Initial larviposition rate (larvae/2 days)	11±3	8±3	10±2	8±3
Total larvae deposited	43±9	24±4	39±11	21±3

As before, current attendance by ants accelerated the aphid's growth, development and initial (two-day) larviposition rates. It also increased the total number of larvae they deposited on the plants, again in spite of the average attended adult spending less time on the plants owing to more of them wandering off after the first few days. These immediate effects of current ant-attendance were greater than any delayed ones due to previous attendance. But there were some effects on the daughters of pre-imaginal attendance of their mothers, effects which differed according to whether the daughters themselves were attended or not. The mean weight of unattended daughters as new adults was greater when their mothers had been attended than when they had not, by 0·114 mg. ($P<0\cdot001$). Maternal attendance also increased slightly the unattended daughters' growth rate, but this was not significant, for in this experiment maternal attendance did not increase and if anything reduced the rate of development of the unattended daughters. When the daughters were attended, maternal attendance reduced the daughters' new adult weight and growth rate ($P<0\cdot001$ in both cases) without apparently affecting their development rate. Thus ant-attendance produced the most rapid growth and largest adults when there had been no previous attendance by ants. But pre-imaginal attendance of the mothers was no drawback for attended or unattended daughters in terms of their larviposition rate; and that is what governs the overall rate of multiplication given equal development rates.

DISCUSSION

The results show that current attendance by *L. niger* favours the multiplication of *A. fabae* directly, by hastening the growth, development and larviposition of the aphids. Banks (1958) did not obtain faster larviposition as a result of ant-attendance but in his experiments the ant-attendance ceased before larviposition began, and in the present experiments, too, ant-attendance which was confined to the immature stages did not affect the larviposition rate of the resulting unattended adults. It seems probable that the accelerated multiplication depends, as Herzig (1937) claimed, upon the stimulation of faster feeding and excretion by the aphids which Banks and Nixon (1958) have now proved. Provided the absorption mechanism of the aphid's gut was not saturated along its whole length during feeding without ants, then the faster throughput of sap with ants would permit faster assimilation of nutrients from it. Nevertheless it now appears most improbable that the ants accelerate the aphids' feeding or produce all their other direct effects on the aphids merely by " raising the plane of nutrition " and thereby accelerating their excretion, which was mentioned as the " simplest hypothesis " by El-Ziady and Kennedy (1956) following Herzig (1937).

Banks and Nixon (1958) suggest that sap entering the pharynx from the inner opening of the stylet canal is no longer under any pressure from the plant and cannot therefore move on down the alimentary canal unless forced. They suggest it is forced onward by elastic closure of the pharynx upon relaxation of the dilator muscles. This may be so, but the available evidence does not yet exclude the possibility that the sap in the pharynx is still under sufficient residual pressure from the plant to be propelled onward without closure of the pharynx. However, it is likely that the ants do influence the activity of the pharyngeal dilator muscles (whether causing them to relax more often so that the pharynx serves as a force pump, or causing them to remain contracted for longer spells of passive sap flow), because a number of the other effects of the ants seem to be, like rectum emptying, active responses mediated by the aphid's central nervous system and not simple consequences of improved nutrition.

When the aphids began, or ceased, to be attended by ants for the first time on reaching the adult stage, there was an immediate effect on the rate at which they deposited their already-formed larvae (Table IV). Secondly, even when the attended adults became " neglected " by the ants and their excretion was apparently retarded instead of being accelerated (p. 35), and they became restless, their rate of larviposition still continued higher than that of unattended adults (Table VI). Thirdly, the accelerated development of the larvae was not always accompanied by accelerated growth, nor *vice versa* (Table VIII). Fourthly, there were effects on excretory behaviour ; and fifthly, on locomotion : either inhibition of it as Banks (1958) showed (less evident in the present work where the host plants were relatively unsuitable), or excitation of it in " neglected " aphids (Table V and figs. 1 and 2). Finally, the mechanism of form determination over which the ants exercised some control (Table VII, and El-Ziady and Kennedy, 1956), is most unlikely to depend directly on nutrition in aphids since it is known to be a neuro-humoral response in other insects. Altogether, the results suggest that stimulation by ants has a centrally-integrated complex of effects on the aphids, usually enhancing their various "vegetative" functions while antagonising motor ones. To produce all these effects may not demand so much from the ants as might appear at first sight, because there seems to exist in *A. fabae* a central nervous mechanism whereby vegetative and motor functions are linked antagonistically in any case (Kennedy, 1958 ; Ibbotson and Kennedy, 1959). All the other effects might follow, for example, from a simple " tranquillising " (motor-inhibitory) effect.

Ecologically, all the known direct and indirect effects of *L. niger* on *A. fabae* seem such as to contribute to one result : increasing and protracting the given aphid infestation. To this intensive operation in cattle-raising, even the induced wandering of the adult aphids after they have deposited a quota of young will contribute, when unexploited host plants are at hand ; and this will still further postpone the final disappearance of the aphids from the foraging area of the given ant colony.

SUMMARY

1. Current stimulation by honeydew collecting *L. niger* had a direct accelerating effect on the growth, development and larviposition of *A. fabae*, at the same time reducing the proportion of alatae among the larvae deposited.

2. The ants induced wandering by older adult aphids which had accumulated a cluster of larvae around them, and this seemed connected with a prolonged inhibition of excretion in these adults while the ants were collecting honeydew from the larvae.

3. The ants also had some delayed effects on the same or next generation of aphids but these were not so clear or consistent as the immediate effects.

4. Although the ants do evidently " raise the plane of nutrition " of the aphids this in itself is unlikely to explain the whole array of effects, which probably depend upon the existing neuro-humoral response mechanisms of the aphid.

ACKNOWLEDGMENTS

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THE IMMATURE STAGES OF MIRIDS (HETEROPTERA) OCCURRING ON BROOM (*SAROTHAMNUS SCOPARIUS* (L.) WIMMER) WITH SOME REMARKS ON THEIR BIOLOGY

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I. Introduction

It is commonly supposed that closely allied species of similar habits are unlikely to occur in the same habitat, or if they do, their habits are likely to change in some way. Therefore, the occurrence of three closely related species of *Orthotylus* (*O. adenocarpi* (Perris), *O. virescens* (Douglas and Scott) and *O. concolor* (Kirschbaum), of another Orthotyline (*Heterocordylus tibialis* (Hahn)) and yet another Phyline mirid of the same appearance and size (*Asciodema obsoletum* (Fieber)) on the same food plant, *Sarothamnus scoparius*, is a phenomenon of both ecological and evolutionary interest. The first four species are essentially restricted to broom, while the last is also found on gorse (*Ulex europaeus* L.).

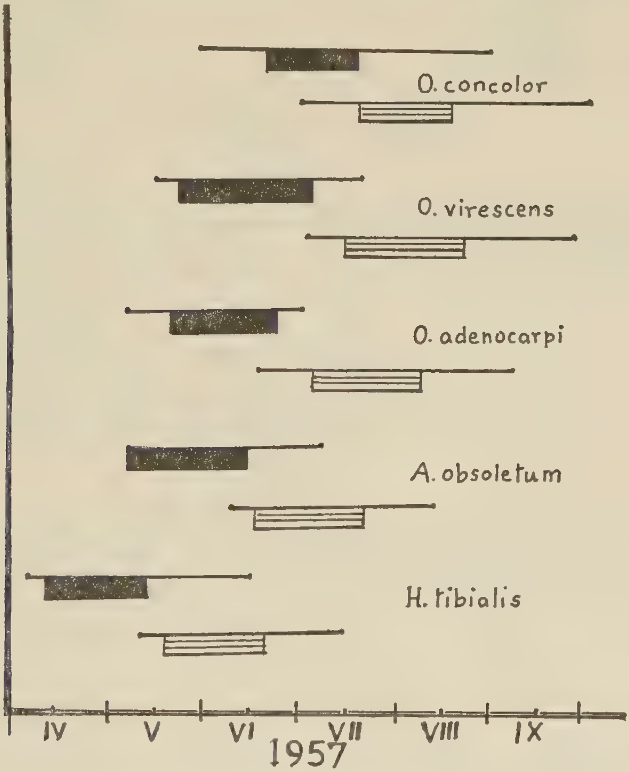
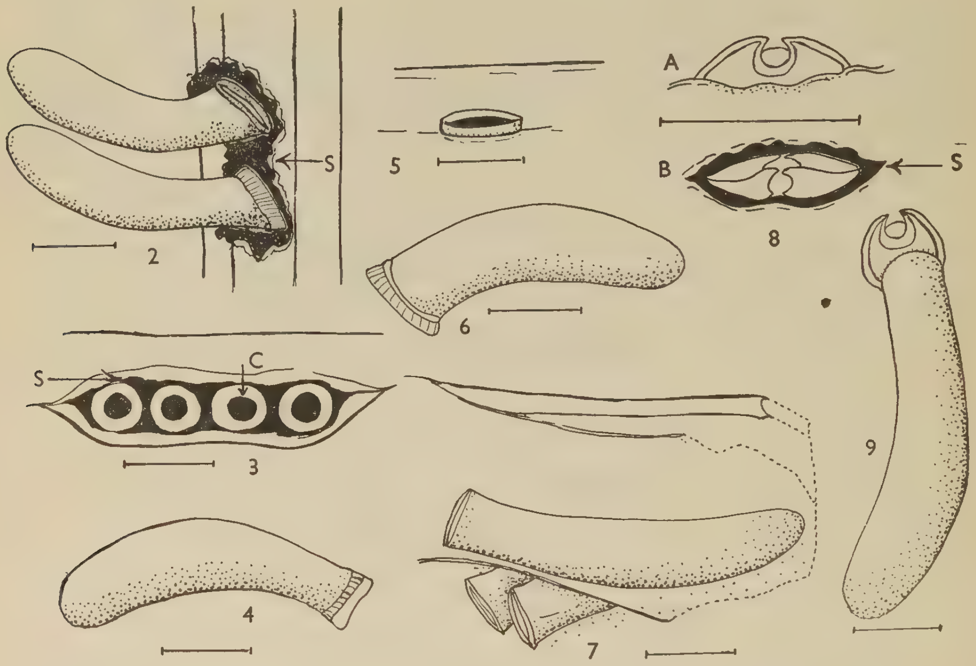


Fig. 1.—Periods of occurrence of mirids on broom (Silwood Park, Berks., 1957). (*Black areas*, times of abundance of larvae ; *stencilled areas*, times of abundance of adults.)

A group of people comprising Professor O. W. Richards, Dr. J. P. Dempster and the present authors hope to study the population dynamics and the interactions of these species and as a first step it was necessary to distinguish the immature stages.

The terminology used in the descriptions of the eggs is that of Southwood (1956*a*). The eggs were first identified in a series of tests in which the mirids were presented with a choice of shoots of different diameters, and the sites of oviposition were confirmed by the examination of numerous cuttings of field broom. The eggs of *H. tibialis* are laid on the sides of the two- to four-year-old stems, while those of *O. virescens* are found on the sides of younger, one-year-old shoots. *A. obsoletum* oviposits in the superficial tissues of the leaf bases of green shoots, while *O. adenocarpi* lays in one- or two-year-old stems, the eggs lying outside the xylem cylinder and often penetrating the buds of the flowering shoots with the operculum lodged in the stem ridge. Most of the eggs of *O. concolor* are found in the lateral depressions below the ridges of young stems. Thus, the oviposition sites of the five species do not overlap to any serious extent and the species also differ in the time of their appearance (*see* fig. 1). Another point of general interest is in the gradual divergence in the lengths of the rostrum of the three species of *Orthotylus* (*see* Table I).



FIGS. 2–9.—(2) *Orthotylus adenocarpi* (Perris), eggs. (3) *O. virescens* (Douglas and Scott). (4) *O. virescens*, egg. (5) *O. concolor* (Kirschbaum), chorion rim of egg. (6) *O. concolor*, egg. (7) *Asciodema obsoletum* (Fieber), eggs (broken lines indicate cut tissues of leaf-base). (8) *Heterocordylus tibialis* (Hahn), chorion rim of eggs (*A*, side view ; *B*, view from top). (9) *H. tibialis*, egg. (*C*, chorion rim of egg ; *S*, scar in stem tissue (Scale line equals 0·25 mm.))

The larvae can be identified by a key (p. 45) that includes other Heteroptera commonly found on broom, and the adults of *Orthotylus* species by one to be found in Southwood (1953). Descriptions of the eggs and larvae of *Anthocoris nemorum* L. can be seen in Sands (1957) and Hill (1957) ; those of *A. sarothamni* Douglas and Scott in Sands (*loc. cit.*), of *Orius minutus* (L.) in Fulmek (1930), and a key and descriptions of *Deraeocoris ruber* L. and *Heterotoma merioptera* Scopoli in Southwood and Scudder (1956).

TABLE I.—*Diagnostic measurements, in thousandths of a mm.*

(Rostrum length in brackets followed by the length of first, second, third and fourth antennal segments).

Larval instar	*Heterocordylus tibialis*	*Asciodema obsoletum*	*Orthotylus adenocarpi*	*Orthotylus virescens*	*Orthotylus concolor*
1st .	(395) 115:175:170:245	(465) 70:120:120:185	(380) 80:150:165:225	(400) 105:175:210:240	(400) 70:130:160:185
2nd .	(530) 140:265:235:255	(555) 80:165:165:215	(571) 90:235:190:250	(450) 130:260:290:270	(480) 120:200:235:230
3rd .	(685) 190:365:300:275	(705) 125:245:245:250	(710) 140:330:250:190	(495) 160:350:360:295	(585) 140:305:320:260
4th .	(865) 205:565:370:275	(965) 145:465:395:305	(945) 205:600:425:375	(610) 215:600:600:350	(755) 200:515:525:325
5th .	(1050) 305:835:485:330	(1220) 215:690:600:380	(1195) 230:920:580:440	(775) 275:875:860:425	(985) 275:860:810:365

II. DESCRIPTION OF IMMATURE STAGES

1. Phylinae

Asciodema obsoletum (Fieber)

Egg (fig. 7)

Delicate, transparent, curved eggs, tapering slightly at base ; rim of chorion narrow, more opalescent than chorion, but somewhat transparent, blending with surrounding plant tissues. Average length (10 eggs) 0·95 mm., greatest width 0·21 mm.

The eggs are not visible externally and in 40 out of the 55 oviposition sites examined, the eggs were laid in the superficial tissues of the leaf bases of the young shoots. In four instances they were found at the junction of two one-year-old branches. A few eggs have also been found in the leaf bases of the older stems. The grouping of the eggs was as follows : 42 were laid singly, 16 were in pairs, and there were three groups of three, one of four and two of five eggs.

Larvae

First instar : pale green, dorsum of thorax and appendages slightly darker ; anterior margin of stink gland opening narrowly brown ; rostrum reaching beyond posterior coxae ; covered with long fine black hairs, the longer ones longer than the basal antennal segment is wide.

Second instar : as first, but with some shorter fine hairs intermixed with the longer ones (fig. 15).

Third and fourth instars : as second.

Fifth instar (fig. 12) : as fourth, but with callosities and posterior margin of pronotum and whole of wing pad suffused with brown, the apices of the latter becoming darker just before the last ecdysis.

2. Orthotylinae

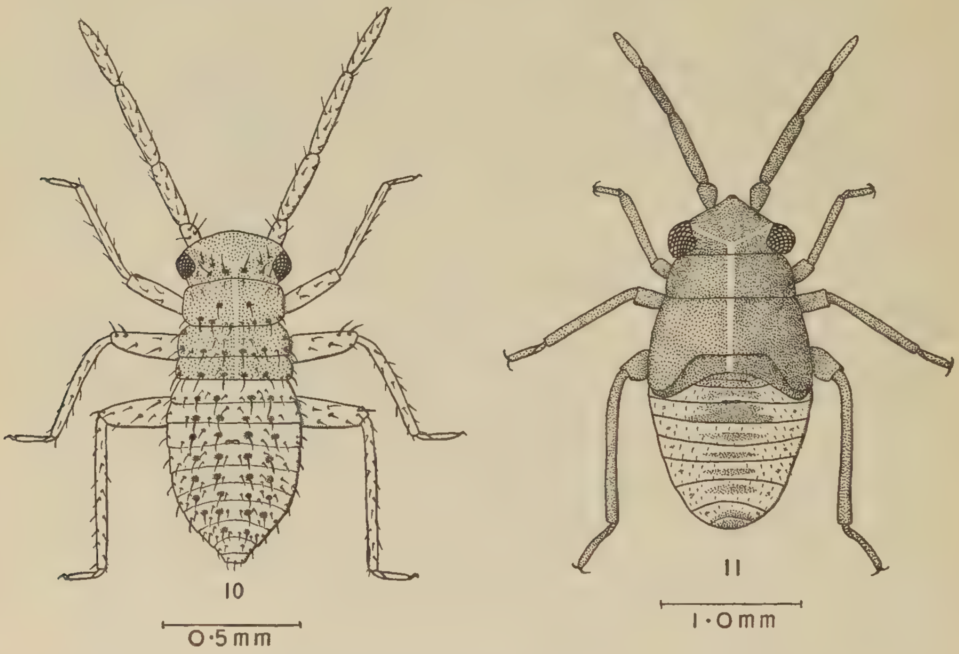
Orthotylus adenocarpi (Perris)

Egg (fig. 2)

Short, strongly curved, tapering gently at base and with a wide, slanting operculum ; chorion transparent, cream, with light brown rim, blending with surrounding plant tissues. Average length (10 eggs) 0·84 mm., greatest width 0·21 mm.

In most instances the eggs were found in one- or two-year-old stems, the exposed rim of chorion in the stem ridge and the rest of the egg lying below the epidermis and outside the xylem cylinder and often penetrating into the flower buds. The eggs were directed at right-angles or at an angle of 45° to the long axis of the stem. The scars left by the ovipositors are often conspicuous and the plant tissues around the eggs have a "bruised" appearance. On drying, the tissues sometimes form brown flaps which conceal the already inconspicuous brown chorion rims. In the older stems (two to four years) the eggs may be laid in the softer tissues of the lateral ridges of the five-sided broom stems. Twelve single eggs were found in these sites; they were laid straight along the ridges with the opercula directed downwards. The eggs have also been found in one-year-old stems, where they formed dome-shaped swellings under the thin epidermis, through which only the opercula protruded.

Forty-one eggs were found laid singly, but three groups of two, one of three and one of four have also been seen.



FIGS. 10–11.—Larvae of: (10) *Orthotylus virescens* (Douglas and Scott), second instar; (11) *Heterocordylus tibialis* (Hahn), fourth instar.

Larvae

First instar: green with dorsum of head and thorax and appendages olive green; margins of opening of stink gland brown; rostrum reaching well beyond posterior coxae; covered with long black hairs (fig. 16).

Second instar: as first, but with rostrum reaching just beyond posterior coxae; covered with long black and a few short black hairs (fig. 14).

Third and fourth instars: as second.

Fifth instar: as fourth, but with the inner margins and apices of the wing pads becoming brown just before the final ecdysis.

Orthotylus virescens (Douglas and Scott)

Egg (figs. 3 and 4)

Short, curved eggs, narrow at operculum and widening towards base; chorion shiny white, tough; rim of chorion tending to be circular, chalk-white. Average length (10 eggs) 0·82 mm., width at base 0·22 mm. and that below operculum 0·16 mm.

The eggs are laid on the one- or two-year-old green shoots, generally in rows, in the incisions made by the ovipositor along the long axis of the stem. The rows of chalk-white chorion rims are conspicuous under a lens, and just visible to the naked eye. The eggs penetrate the xylem cylinder.

The numbers in a group and the numbers of groups found in 1957 are given below :

Number eggs per group .	1	2	3	4	5	6	7	8	9	12
Number groups found .	13	38	56	59	41	26	14	5	2	2

Larvae

First instar : green with dorsum of head and thorax and appendages a dusky olive green, opening of stink gland dark brown ; rostrum reaching beyond hind coxae ; thickly covered with long black hairs—as long as the basal antennal segment is wide and arising from dark brown spots.

Second instar (fig. 10) : as first, but with long and short black hairs (fig. 13).

Third instar : as second, but rostrum just reaching hind coxae.

Fourth instar : as third, but rostrum reaching mid-coxae.

Fifth instar : as fourth, but apex and inner margin of wing pads becoming dark brown before the final ecdysis ; rostrum not quite touching mid-coxae.

Orthotylus concolor (Kirschbaum)

Egg (figs. 5 and 6)

Short curved eggs, slightly tapering at base, with a slanting, wide operculum ; chorion transparent, whitish ; rim of chorion white. Average length (10 eggs) 0·82 mm., greatest width 0·24 mm., and that of operculum 0·21 mm.

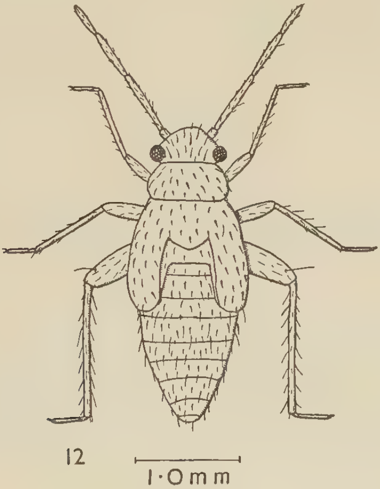


Fig. 12.—*Asciodema obsoletum* (Fieber), fifth instar larva.

Most of the eggs are laid in the two-year-old green stems, more rarely in the shoots which have grown in the current year. The sites of oviposition are mostly in the depressions below the lateral ridges of the five-sided broom stems. The eggs are laid singly, although several may be laid along one side of a stem at short distances from one another. Internally they penetrate the xylem cylinder, externally the elliptical white chorion rims are visible, even to the naked eye, but they are not as conspicuous as those of *O. virescens*.

Larvae

First instar : green with dorsum of head and thorax and appendages olive-green ; opening of stink gland brown ; rostrum reaching well beyond posterior coxae ; covered with long black hairs—but these not arising from black spots.

Second instar : as first, but with numerous shorter hairs present between the longer ones.

Third instar : as second, but olive-green of dorsum of head and thorax not as distinct from general coloration.

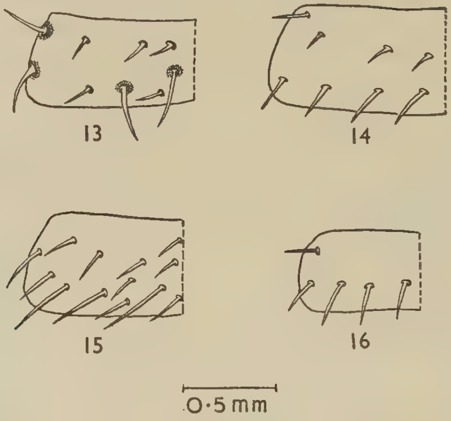
Fourth instar : as third, but now more thickly covered with long hairs as long as basal antennal segment is wide, and shorter black hairs, the former sometimes arising from very small light brown dots.

Fifth instar : as fourth, but apices only of wing pads becoming dark just before final ecdysis ; opening of stink gland light brown.

Heterocordylus tibialis (Hahn)

Egg (figs. 8 and 9)

Curved and asymmetrical, broadly rounded at base, whitish rim of chorion drawn out into 2 incurved processes ; chorion tough, transparent, creamy-white. Average length (10 eggs) 1·09 mm., greatest width 0·28 mm.



FIGS. 13–16.—Left-hand side, dorsal aspect, second thoracic segment to show chaetotaxy : (13) *Orthotylus virescens* (Douglas and Scott), second instar larva ; (14) *O. adenocarpi* (Perris), second instar larva ; (15) *A. obsoletum* (Fieber), second instar larva ; (16) *O. adenocarpi*, first instar larva.

The eggs are laid mostly in two to four-year-old green stems ; none have been found in the softer one-year-old shoots. The delicate and inconspicuous chorion rim projects above the stem epidermis, while the rest of the egg penetrates deeply into the xylem cylinder. The scars made by the ovipositor are small and inconspicuous. Most of the eggs are laid singly or in pairs and of the 78 examined, 22 were laid singly, 34 in pairs and the rest in groups of three or four in a common incision.

Larvae

First instar : bright red with head and dorsum of thorax, except for a Y-shaped central line, margins of coxal cavities, margins of stink gland opening, posterior of abdominal segment 10, all segment 11 and anal cone dark brown ; rostrum reaching well beyond posterior coxae ; sparsely covered with short and a few long black hairs.

Second instar : as first, but with a distinct white line under eye and on outer margins of thoracic segments ; coxae and pleurites banded with white ; trochanters white ; area of abdominal segments 2–9 with a brown median blotch, and segments 4–9 with a brown lateral dot also, rostrum only just reaching posterior coxae.

Third instar : as second, but with dark markings on dorsum now almost black ; white banding of coxae and pleurites more marked and apical segment of antennae slightly paler than the rest.

Fourth instar (fig. 11) : as third, but pleurites and ventral surface of head largely white and lighter parts of abdomen more greenish-red.

Fifth instar : as fourth.

III. KEY TO LARVAE

The instar can be determined by reference to the degree of development of the thorax, as described by Southwood (1956*b*). The first and second instars are most conveniently separated in the green species by the presence of only one length of hair in the first instar, whereas in the second there are numerous additional shorter hairs. Determinations of the more important species should be checked by reference to the diagnostic measurements (Table I).

1 Green or green and brown 2
– In part or entirely red or black or entirely brown 5
2 Longest hairs arising from brown spots, less marked in first instar ; in later instars rostrum short, not reaching third coxae **Orthotylus virescens** Douglas and Scott
– Longest hairs not arising from brown spots ; rostrum reaching just or well beyond third coxae 3
3 Opening of stink gland not easily visible, with only anterior margin narrowly brown ; pubescence of long fine hairs (fig. 15), all as long as basal antennal segment is wide, some much longer ; claws of phyline type with hair-like arolia . . . . **Asciodema obsoletum** Fieber
– Opening of stink gland easily visible, margins deep brown ; pubescence of shorter hairs, much shorter than basal antennal segment is wide ; claws of orthotyline type with convergent flap-like arolia 4
4 In second-fifth instars, third antennal segment distinctly shorter than second; in fifth instar, ratio of third : second less than 2 : 3 **Orthotylus adenocarpi** Perris
– In second-fourth instars, third antennal segment longer than second, in fifth only slightly shorter . . . . **Orthotylus concolor** Kirschbaum
5 Three dorsal abdominal glands 6
– Less than 3 dorsal abdominal glands 8
6 More ovoid ; yellow-brown or olive-brown . . . . **Orius** spp.
– More elongate ; yellow-brown or reddish 7
7 In third-fifth instars apices of wing-pads pale . . . **Anthocoris nemorum** L.
– In third-fifth instars apices of wing-pads deep reddish **Anthocoris sarothamni** Douglas and Scott
8 Two dorsal abdominal glands; in later instars, head with spinose projections; first and second antennal segments about equal to fourth **Dictyonota fuliginosa** Costa
– One dorsal abdominal gland : head without spinose projections ; second antennal segment greater in length than both first and fourth 9
9 Body covered with clavate hairs (deep reddish-purple; last abdominal segment tubular) . . . . **Deraeocoris ruber** L.
– Body not covered with clavate hairs 10
10 Elongate in form ; antennae longer than total body, not thickened **Miris striatus** L.
— More oval in form ; antennae not longer than total body, second segment thickened, especially in later instars 11
11 Antennae in part pale yellowish or whitish, second segment strongly thickened in third-fifth instars . . . . . . **Heterotoma merioptera** Scopoli
— Antennae entirely dark red or brown-black ; second segment only slightly thickened in fourth and fifth instars . . . **Heterocordylus tibialis** Hahn

IV. ACKNOWLEDGMENTS

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A SIMPLE APPARATUS DEMONSTRATING THE STYLET ACTION OF A PLANT BUG

By P. W. Miles

(*Waite Agricultural Research Institute, University of Adelaide*)

Cinephotomicrographic studies of the stylet action of the milkweed bug, *Oncopeltus fasciatus* Dall. (Miles, 1958), have shown that the direction in which the stylet-bundle advances in media is related to the order in which the individual stylets move forward. When the maxillae advance, either alone or in company with one or other of the mandibles, progress is always straight, whereas when either mandible advances alone, it curves inwards and the other stylets subsequently follow this curve. Isolated mandibles have a natural inward curve at the tip, and the model described below was made to test the possibility that the direction taken by the advancing stylet-bundle is a simple consequence of the mechanical properties of the stylets and depends only on their sequence of movement.

The stylets were represented by strips of 0·02 inch thick polyvinyl chloride (*PVC*) sheet, 1 cm. × 18 cm. and rounded at one end. The strips representing the mandibles were softened over a flame at the rounded ends and curved as shown in

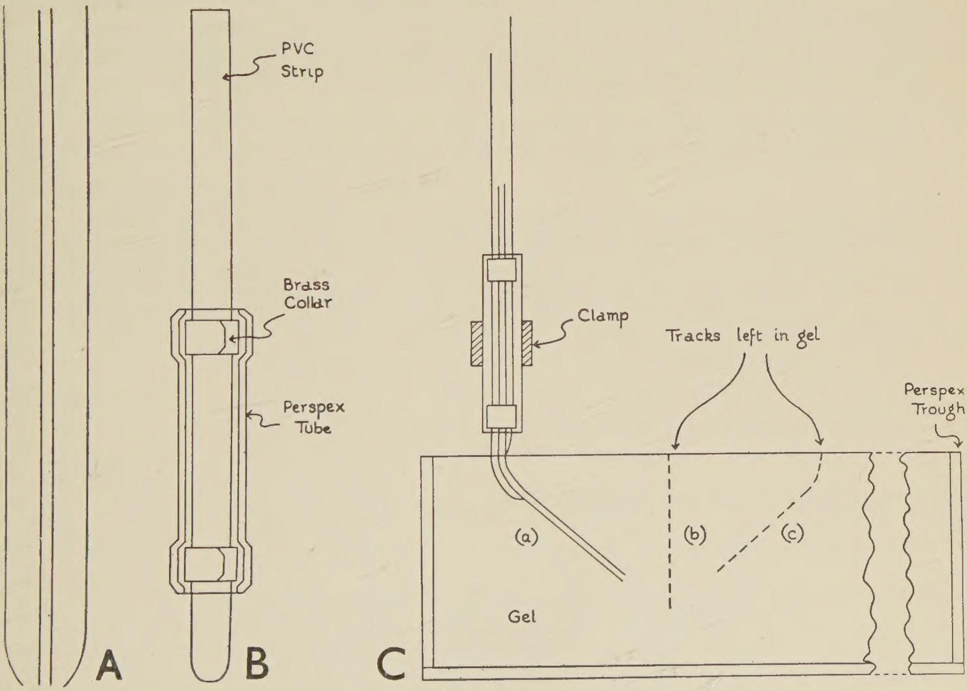

Fig. 1.—Diagrams of an apparatus which demonstrates the stylet action of *Oncopeltus fasciatus*. (*A*) Profiles of the four " stylets ", made of *PVC* strips; the inner and outer strips represent the maxillae and mandibles respectively. (*B*) The " stylet " and " rostrum " assembly, viewed with the " stylet "-strips face-on. (*C*) The apparatus set up for demonstration. When either " mandible " is pushed into the gel, it is deflected inwards, and when the other " stylets " are then pushed down, they are guided to the one side (*a*), (*c*); if the two " maxillae ", either alone or in company with either mandible, are pushed into the gel, progress is straight down (*b*).

the accompanying diagram. The four strips were bound together by two collars of thin brass strip so that the " stylets " were held firmly but would still slide over one another easily. The ends of a 3-inch length of $\frac{1}{2}$-inch bore perspex tubing were softened by heating and the collars set into them as shown. The tube, which represented the insect's rostrum, was then clamped vertically above a 10 per cent. gelatine gel.

The " stylets ", when pushed into the gel, behaved as predicted : it was found that only a slight curve at the tip of a " mandible " was sufficient to guide it into a strongly curved path within the gel, and when the other " stylets " were then depressed, the gel held the " mandible " in position and the other " stylets " followed the curve ; on the other hand, when a " mandible " was pushed down together with the " maxillae ", the latter overcame the tendency of the " mandible " to curve inwards, and progress was straight into the medium.

The apparatus proved useful for classroom demonstrations. For this purpose, the " mandibles " and " maxillae " were painted different colours and, since the maxillae naturally move as a unit, their counterparts were stuck together with the paint while it was still wet. A container for the gel, which permitted several successive demonstrations, was made by cementing together pieces of $\frac{3}{16}$-inch perspex to form a trough 18 inches long, 1 inch wide, and $3\frac{1}{2}$ inches deep.

REFERENCE

MILES, P. W., 1958, The stylet movements of a plant-sucking bug, *Oncopeltus fasciatus* Dall. (Heteroptera : Lygaeidae). *Proc. R. ent. Soc. Lond.* (A) **33** : 15–20.

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